THALASSIOPHYTA
AND THE SUBAERIAL TRANSMIGRATION

By

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I

THE ORIGIN OF LAND-FLORA, AND THE SO-CALLED ANTITHETIC ALTERNATION

The beginnings of Botany are in the sea; and as it becomes more obvious that the vegetation of the land has at some time originated from transmigrant marine phytobenthon, and that the somatic organization of branched cellular axes, stem and root, with apical growth and mechanism of leaf-arrangement, as also the entire phenomena of space-form, are the *inherited equipment* of a preceding phase of existence in the wholly submerged environment of the sea;—while the cell-equipment of chloroplasts, starch-metabolism, flagellated gametes, nuclear phenomena, chromosomes, sexual reproduction and meiosis, are equally *inherited mechanism of a still older phase* of pelagic phytoplankton, persisting practically unchanged throughout the benthic period,—it becomes necessary to present some mental picture, however sketchy and crude, of the means whereby such a transition may have become possible, at some early period of the world's history. Since there is no indication whatever of any such migration being effective at the present time; and the very generally accepted convention of the evolution of the 'Sporophyte' generation of Land-Flora, as a 'post-sexual phase,' arising *de novo*, to repeat the entire sequence of somatic development in much the same style, has been regarded as peculiarly futile and mistaken. Since, again, it seems almost inconceivable that organism developing in response to the wholly new complex of stimuli associated with subaerial environment, could ever reproduce fundamentally the same effects as have been already initiated in response to the very special conditions of gas-supply, food-salt, and light-supply of the sub-littoral zone. *Homoplasy* is a favourite saving expression with many morphologists; but homoplasy does *not* imply the identical moulding of organism under diametrically opposed conditions of environment. If some working hypothesis be necessary, the antithetic theory is better than nothing at all; and for fifty years it has dominated the botanical outlook (1851–1908), and has afforded an effective stimulus to research.[1] The only effective criticism is the establishment of an alternative point of view; and those, to whom the surprising adventures of an 'intercalated post-sexual phase' may not appeal, are naturally expected to provide something more rational.

It may however be noted that:—

(1) The subject has obvious limitations.

(2) No absolute answer is perhaps ever possible.

(3) Since in no case can there be direct phylogenetic progression.

(4) Observations are necessarily restricted to a few quite disconnected types.

(5) These being cut off behind ,at different morphological horizons, and at present existing as 'blind-ends.'

(6) The existing races are only significant as affording suggestive evidence, and as expressing the solution of similar problems by phyla of different origin.

(7) The scientific value of such discussions consists in the isolation of the individual factors, whether vestigial or adaptational, at their proper

[1] Bower, 'Origin of a Land-Flora' (1908), p. 244.

value in the story; so that the solution of the entire problem may be viewed in due perspective.

(8) The problem is not that of apparently uncalled-for '*sterilization*', but one of '*physiological engineering*', based on the supply of energy and food-material to living mechanism, in quantity sufficient to enable it to grow, and to produce reproductive units; the latter again in quantity sufficient to counter-balance the inevitable wastage due to the conditions of a new phase of existence.

The erroneous outlook of the 'Theory of an Antithetic Alternation of Generations', which has led to such a curious misconception of the problem of the origin of land-vegetation, is much more deeply seated than appears at first sight; the theory so far is admittedly the natural historical development of the general lines of botanical research of the middle nineteenth century, based solely on the consideration of the simpler forms of Vascular Cryptogams and Bryophyta, as types of Archegoniate affinity, and affording the simplest apparent solution of the problem of the plant-kingdom, as traced from the only means at the disposal of the earlier exponents of Modern Botany.

It was to Hofmeister,[1] working as a young man, an amateur and enthusiast, in the early morning hours of summer months, before business, at Leipzig in the years before 1851, that the vision first appeared of a common type of Life-Cycle, running through Mosses and Ferns to Gymnosperms and Flowering Plants, linking the whole series into one scheme of reproduction and life-history; based on a rhythmic sequence of sexual and asexual phases, constituting the 'Alternation of Generations', so long regarded as almost *a mystic property of plant-life*; the origin and exact significance of which remained wholly obscure. But though the existence of such an alternation of generations in Land-Flora is a definite and remarkable *fact*, the question of the *origin* of these phenomena is a perfectly distinct problem, and has no necessary connexion with the origin of Land Vegetation; the initiation of the process being traced in marine organism, of which Hofmeister unfortunately knew nothing. It may be noted that these conceptions were Pre-Darwinian, and not necessarily phylogenetic in a modern sense; but they prepared the way for evolutionary standpoints, as applied to the plant-kingdom, and have afforded, in fact, the great central clue to the *subsequent* and more modern development of the Flora of the Land, without necessarily adducing anything of its ultimate origin. Apart from the chain of thought established by Hofmeister (1851), to dominate Botanical work for two succeeding generations, may be noted the general tendency of the systematists of the age to classify all groups of the plant-kingdom, beginning with the smaller and more insignificant types, and working up to phases of greater complexity, as affording the simplest mode of expressing the *ascent* of living forms in the scale of existence, comparable with the position of Man at the head of creation. The method suited an idealistic and philosophical conception of 'progress to perfection', as well as the crudest attempt at grasping views

[1] *Wilhelm Hofmeister*, born 1824, died 1877, of Leipzig, Professor at Heidelberg (1863–76). 'One of the finest botanists of Germany, as a man of distinguished gifts, of great energy and application, and of remarkable powers of presentation.' 'His appearance had in it nothing of the Germanic type; he looked like a Southern Frenchman' (Pfitzer). 'Not merely an active and industrious man of learning, but a real genius, such as appear in science only between long intervals of time' (Goebel).

Cf. Hofmeister, 'Vergleichende Untersuchungen', Leipzig (1857); Eng. Trans. with additions, Currey, Ray Soc. (1862): Goebel, 'Plant-World' (1905), p. 291, with portrait.

of more modern evolution; and in the latter interpretation the method survives to the present day.

Thus the simpler forms of Thallophyta are classified by placing the unicellular algae at the beginning of the series, and working up to the more complex; and in view of the older plants of the discrete plankton-phase this in general cannot be disputed, though the case of the Desmid may be left an open question.[1]

Bryophyta begin with small vague thalloid Riccias, leading up to the development of foliose Jungermannias, and the radial erect Mosses with complex sporogonia.[2]

A similar method applied to Flowering Plants would with equal acumen place Pond-forms as *Wolffia* and *Lemna* at the base of the Angiospermous series; and though this view is not accepted at the present day, it is nevertheless a fact that Eichler's views on Systematic Botany remained at this level; and in his classical 'Blüthendiagramme' (Leipzig, 1875)[3] *Wolffia* is the initial type.

Again in dealing with groups of Algae, Oltmanns (1904) places all 'simpler' forms at the beginning; as the more simple the greater the certainty of a flagellate connexion: no allowance is made for regression at any point; and this is only hinted at in cases of most obvious parasitism.

To Hofmeister working at Leipzig and Heidelberg, in ignorance of the sea, the progression of plant-life was viewed from the *standpoint of the fresh-water pond*, and in the light of a transition from the medium of fresh-water and seasonal vegetation to the arboreal vegetation of the North Temperate Zone, as displayed in Central Europe. The method has its obvious limitations.[4] Hofmeister's text-book had been the immortal 'Grundzüge' of Schleiden, and this contained only scathing remarks with regard to Marine Algae, which the latter knew only from shrivelled herbarium specimens, probably of no great size:[5] while Sachs ('Lehrbuch', Leipzig, 1870) again

[1] 'Engler-Gilg Syllabus' (1912): West (1916), 'Algae', vol i, p. 377.

[2] Schiffner (1893) in 'Engler and Prantl'; Sachs (1870), 'Text book'; Revision by Cavers, New Phyt. (1910) p. 81, (1911) p. 84; 'Phylogeny', p. 41.

[3] The 'Blüthendiagramme' of Eichler (1875–78) is perhaps the only noteworthy German work on Botany which has not appeared in an English version. A translation by H. E. F. Garnsey (Oxford) was never published: the peculiarly archaic standpoints in floral morphology tending to obscure the presentation of an otherwise invaluable collection of details.

[4] 'The phaenogams therefore form the upper terminal link of a series, the members of which are the Coniferae and Cycadeae, the Vascular Cryptogams, the Muscineae, and the Characeae' (!), Hofmeister (1862), p. 439.

[5] Schleiden, Eng. Trans. Lankester (1849). References to sea-weeds are of the most meagre and contemptuous description (six pages for Algae, including fresh-water types). Cf. p. 146. How far a botanist could go, who had never seen the sea and its vegetation, is neatly expressed in the following criticism:—'My views on this subject are fully concurred in by Kuetzing (1843), who after thirteen years' laborious study declares that there are no *species*, but merely *forms* of Algae; and these he has followed throughout the whole course of their development, showing in many cases by careful observation, although in a confused manner, that they are devoid of an independent existence. The terminology in use at the present time with respect to the Algae is a mere confusion of words; and I may wholly dispense with all these empty terms. Kuetzing, who has carried the fabrication of words beyond all limits, makes use of seventy terms (i.e. *genera* of the 'Phycologia Generalis', 1843) for the different *forms* of the family of the Algae.'

On p. 149, however, the cause of the ignorance of marine Algae is admirably expressed, and still contains much truth:—'In some degree, certainly the cause lies in the artificial senseless methods of research that infect the whole Science of Botany, which has hitherto directed its attention far more to herbaria than to living plants;

affords a good idea of the outlook of a landsman, and continues the tradition of ignoring sea-weeds;[1] even the current edition of 'Strasburger's Botany' (Eng. Trans., 1912) conveys the impression that marine algae are of very subsidiary importance, and plants of no great mass, either as individuals or as races.[2] Hence it is not surprising that Bower, whose volume on the 'Origin of a Land Flora' (1908) affords such an admirable summary and continuation of the standpoints of the Hofmeister school, should also refuse to discuss them[3].

Conclusions.

(1) The Theory of an Antithetic Alternation of Generations was originally elaborated by continental botanists in unavoidable complete ignorance of the facts of marine vegetation as a preceding phase of plant-organism.

(2) It is thus based entirely on the contemplation of the surviving Archegoniate record (Hofmeister, 1862, p. 439; Bower, 1908, p. 256).

(3) The theory confused two entirely different problems, which though apparently inextricably blended, are now seen to be perfectly independent;—as (i) The translation from aquatic to subaerial conditions, and (ii) The evolution of a cytological and morphological alternation of generations.

(4) The latter has been very generally regarded as the outcome of the former; even to the extent of regarding such translation as a causal factor.

(5) If plant-life began in the sea, it may be as well to know something about the life of sea-weeds.

and hence those who live far inland become Algologists (cf. Schmitz of Greifswald), while botanists residing near the sea-side busy themselves in describing some little dried *Jungermannia* from Java; and European investigators thus too often devote more attention to tropical plants than to those that are indigenous to their own country, and are in their own immediate neighbourhood.' Similarly the most critical work on the commonest indigenous sea-weed of our shores (*Fucus vesiculosus*), as also the Floridean *Polysiphonia violacea*, has been done by a Japanese (Shigeo Yamanouchi) at Chicago; and this applies still more to the case of *Cutleria*, which grows on the Channel coast, but not in America at all. Similar data are still lacking for the first sea-weed at the high-tide mark (*Pelvetia*), as again for many other British plants; though many of the most common forms, as *Fucus serratus* and *Saccorhiza*, are unique monotypes with restricted distribution, nowhere so good as on our own coasts (cf. Spence, 1918, Journ. of Bot. p. 281, 'Laminarians of Orkney'). The same applies with even greater force to the wonderful weeds of British Colonies, as Tasmania, Western Australia, New Zealand, and the Falklands (*Lessonia*, *Durvillaea*). It is not generally appreciated that these 'uncouth' growth-forms represent a type of vegetation of the sea, in all probability unaltered to any extent since before the geological record began, and presenting in their organization the solution of the botanical problems of an otherwise unknown world of the past.

[1] Sachs (1870) gives only the barest account of *Fucus* from Bornet and Thuret, with some minor Florideae from Naegeli (1861). The plants are treated as of interest solely from the standpoint of sexual fertilization, and as if on a perfect equality with *Oedogonium* and *Coleochaete*, with which they are sandwiched. It is just mentioned that the larger algae (*Fucus*) may be several feet long (but so are forms of *Chara* and *Thorea*), p. 223. Sachs only knew the sea from holiday trips to Ostend.

[2] Eng. Trans. (1912), p. 367. A sketch of *Macrocystis* from Skottsberg, of a diminutive 'older thallus', as a five-inch figure ($\times \frac{1}{80}$), attempts to avoid exaggeration and visualize a plant that commonly grows 100 yards long, as a 'breakwater' type of vegetation.

[3] 'The Thallophyta may be left on one side . . . at present they have only a remote, and chiefly a theoretical connexion with the question of the origin of a Land-Flora' (p. 256.)

THE HYPOTHETICAL LANDWARD MIGRATION

In addition to the bias of Continental schools of Botany[1] already noted, additional probability of a migration to land, *via* estuaries and rivers to the conditions of fresh-water swamps, appears to follow naturally from the zoological parallel of the apparent landward migration of Mollusca, Insecta, and higher Vertebrates; many of these having been assumed to have followed the same route, for the simple reason that (1) the mouths of rivers are the natural gateways from the sea, and inland waterways afford a means of rapid and peaceful penetration of the land-area; while (2) direct access from oceanic water, owing to tidal phenomena and the effect of wind-produced wave-action, is almost always prevented by a barrier of cliffs, dunes, or beach, rendering the transition from one phase to the other abrupt and inhospitable.[2]

The actual area of the littoral zone, even including the sub-littoral, is so small in relation to the masses of sea and land, that it affords little scope for mass-migration; although within its narrow field competition may be more severe than in any other biological station (Darwin). But the hypothesis that plants have necessarily followed the lines of more recent animal migration demands that other factors be taken into account. The animal follows its food, and given a food-supply, is largely independent of the quality of the medium: numerous examples may be found of fishes passing freely into rivers in search of food (cf. eels).[3] The autotrophic plant is wholly dependent for its food-salt supply on the chemical content of the water; and this in the case of 'fresh' water as opposed to salt is strikingly inferior. River and lake waters of Europe average only $\frac{1}{200}$ of the salt-content of the sea; nor need they be any richer in the essential supply of nitrate and phosphate. Phenomena of malnutrition, consequent on withdrawal from the open sea, are the most characteristic feature of estuarine and salt-marsh vegetation.[4] There is no evidence of any landward

[1] Or rather German, since the conception of the origin of land-vegetation from marine algae was familiar to French Algologists from the time of Lamarck and Bory de St. Vincent, who had described the arborescent Lessonias of the Southern Seas (Voyage of 'La Coquille', 1826); cf. also Landsborough (1851), 'British Seaweeds', p. 80, on atheists.

[2] Minor examples may occur, as Marine Mollusca leaving the tide-range and feeding above the tide-level (*Otina*), *Codium tomentosum* extending to a bog (Harvey), or *Fucus muscoides* growing on peat in a similar situation (Cotton); *Catenella* and *Bostrychia* extend among higher vegetation in the Mangrove-swamps of the Tropics; but they do not reproduce there, and the migration is so far incomplete.

(Cf. Baker and Blandford (1916), J. L. S., p. 325, 'Brown Seaweeds of the Salt-Marsh').

[3] The eel from the deep Atlantic (500 fathoms) ascends rivers and even travels over land, devouring spawn and decomposing relics of higher organism, but does not become terrestrial. The salmon ascends rivers to breed in quiet sheltered water at a higher temperature, but does not feed. (Calderwood, 1908, 'Life of the Salmon'.) Quiet water of higher temperature would be similarly an inducement to plant-forms, if the food-problem could be solved.

[4] All fresh-water plankton is on a lower plane in size, variety, and abundance; and the same applies to all pond-life as compared with the sea. Fresh-water presents

migration *via* estuaries among plants which have attained any considerable size; on the contrary, everything goes to suggest the influence of fresh-water as an extreme reducing-factor; and the green algae surviving in fresh-water are somatically the merest depauperated relics in the last phases of deterioration, as reduced filamentous and disc-types.[1] So far as direct migration of plant-life from the sea is concerned, the door is closed. To pass from the sea to fresh-water implies starvation and deterioration of the output of reproductive cells, and hence failure to compensate the wastage of the race, and extinction.[2]

While there is no evidence of any such migration taking place at the present time, the same factors would militate against it having ever operated in the past. The pleasing idea of the prototypes of the Archegoniatae[3] following the rivers to vegetate on mud-flats, as possibly suggested by the adventures of the Mud Fish (*Protopterus*), usually regarded as expressing a phase in the evolution of the land amphibian, there similarly to undergo the strain of seasonal desiccation, will not work.

Transmigration to the land cannot even postulate the existence of mud or estuaries; rivers imply the long-continued denudation of vast continental areas: and such a continental area could not have been lifted out of the sea in the first place without taking some life with it; the point is, what did it

little food-supply except at spawning time: insects and worms are a poor substitute for plankton. (Cf. West, 'Algae', 1916, on Pond Plankton.) Fresh-water fishes are more able to endure hunger than marine fishes (Günther).

[1] Cf. *Coleochaete*, *Oedogonium*, *Vaucheria*, *Nitella*, *Batrachospermum*, *Thorea*, *Lemanea*, *Hydrurus*: *Chara* alone as an exceptionally massive form is suggestive of direct migration *via* standing lagoons (*C. baltica*).

[2] Cases of suggested migration occur only in depauperated types (*Lemanea*), and a few examples suggestive of migration by the agency of aquatic birds (*Batrachospermum*, *Phaeothamnion*, *Lithoderma*); all small and of the lowest grade in their respective series. The migration of a mobile zoïd, or passive spores, in any stream, *against the current*, presents considerable difficulties; and the case of *Lemanea* with its *Chantransia*-stage suggests migration by the agency of fish (or aquatic animals). Leechman (1916) has found a *Chantransia*-like Floridean growing under the Barracarra Falls (British Guiana) sixty miles from the sea, and wholly asexual.

[3] Cf. Bower (1890), Annals of Botany, iv, p. 362, for picture of the origin of the sporophyte as the 'natural outcome' of the migration from water to the land.

The biology of such tropical Mud-fishes has apparently exerted a controlling influence on hypotheses of similar seasonal change being responsible for the antithetic origin of the alternation of generations in Bryophyta. But, it may be noted, that no such seasonal changes can be postulated for remote geological epochs; the conversion of the swim-bladder of a fish into a lung has no direct reference to perennation over a dry season, but is the response to existence in stagnant and non-aerated water (Günther); as also alternation of generations has been undoubtedly evolved in plant-organism which has never left the sea. The progression of amphibia from mud-fish may be thus illumined by the organization of Dipnoi, so far as the latter illustrate the fate of residual fishes of the transmigration left in standing pools, diluted by rain-water, to live as best they can on decaying vegetable débris or lower animal life; though, as transmigrants in danger of starvation, the evolution of ambulacral limbs is much more important than an air-breathing lung, and the first amphibians contemporary with the first land-plants present no suggestion of later migration *via* rivers.

It may be also noted that the fins of *Ceratodus*, as bilateral anisophyllous laminae, repeating in miniature the metameric segmentation of the main axis, are the nearest approximation to 'ramification', in the botanical sense, found in any early type of high-grade animal, and express a curious parallelism with the general principles of the organization of the axes of many marine algae.

take? The investigation of modern marine algae shows what sorts of autotrophic organism can be evolved in the sea, and these undoubtedly express the possibilities of the equipment of marine phytobenthon available then as now. As the highest type of marine animal (the vertebrate fish) led on to the higher animal organism of the land, so land-flora has been undoubtedly produced from the highest plant-organism attained in the sea.

An unfortunate though formerly excusable bias of the pseudo-evolutionist school in favour of 'links', is responsible for much confusion of thought in phyletic deduction, in that everything was expected to link on to something else; and attempts are still made at constructing absurd phylogenetic trees, just to contain a few residual races of the present world. The futility of this method is at once apparent when it is grasped what a small proportion the living representatives of the present world bear to the races that have vanished; just as the few specimens of the geological record afford but the merest glimpse of the life of the ancient world. The modern Christian era may be said to cover less than 1% of the time the human race has existed physically very much the same as at present. One must be prepared to admit that this period may not cover more than one to one-tenth per cent. of the geological fossil record from Tertiary to Silurian (20–200 millions), which implies a denuded land-surface; and what relation such a period may bear to the entire range of plant-organism, from the monad which has all the essentials of physiological functions as a cellular organism, and even beyond this to the time when life first attained the condition of mere ultra-microscopic particles from the complex medium of sea-water, is beyond any possibility of human computation: two thousand millions may be suggested.[1]

It is understood that we have to make the best of given inadequate material, but the point is to recognize its limitations, and to keep a clear sense of proportion.[2] There is no need ever to wonder at a race dropping out, or being sharply 'cut off' behind: the phenomena of 'wastage' involved in the assumption of benthic habit, when fully appreciated, afford ample grounds for the elimination of any race at any time: few phyla of plants in open competition of optimum environment can be said to do more than live at present on a narrow margin; and though individuals or the race may apparently persist almost indefinitely by means of vegetative propagation under special circumstances (Gulf-Weed, *Thorea*, *Rhodochorton*, Fuci of the Salt-Marsh), this so far as is known does not make for progress in the evolutionary sense. There is no reason to suppose that the wastage of early Land-Flora was any less than that of the preceding submerged condition; it was in all probability infinitely greater, though felt in a new direction (wind-borne spores).

[1] For possible age of the earth, cf. Jeffreys (1918), 'Nature', p. 273, suggesting 3,000 millions for the earth's existence as a separate planet; older speculations in Osborn (1918), 'Origin and Evolution of Life', pp. 29, 36; Sollas (1906), 'The Age of the Earth', p. 25. Speculations on the rate of denudation, or on the addition of salt to an ocean of distilled water, are merely tedious.

[2] A very inadequate account of the origin of the world, related by Sumerian migrants of the Euphrates delta, based on a comparison of the climatic conditions of Mesopotamia with those of the tropical forest of India, as seen through the haze of inherited folk-lore, has had a remarkably persistent effect on human literature; and similarly Hofmeister, in studies of local pond-life, was doing the best he could with the material at hand in S. Germany. But the origin of life, and its progression, must have been on a far wider horizon. The story involves not only the sea, but the tropics, where life moves more rapidly with increased temperature and insolation. The ultra-orthodox botanist may have much in common with an orthodox theologist.

Among marine algae there have been possibly only the merest insignificant changes during the entire geological epoch. The marine types from which the first Land-Flora started may quite well have been recognizably the same sort of plants to look at that are common on oceanic sea-boards at the present day. *Chara* may go back unchanged as *Chara* to the Trias at least; *Durvillaea* as a Fucoid with oogamic conceptacles is to look at no different from a Laminarian on which one would expect to find isogamous gametangia. The Florideae present an organization and life-cycle recognizably far more complex and biologically 'higher' than that of the Phaeophyceae, and of these the calcified Corallinaceae afford again quite high-grade expression as a very special line; yet 'reduced' Lithothamnions of this series, indistinguishable from those of the present day, were rock-building algae of the Cretaceous; and identification only fails in earlier strata owing to the natural chemical and physical disorganization of the material.[1]

With such remote antiquity, even the highest algal groups show an isolation beyond recall. The Florideae are the most narrowly circumscribed, as they are also in many respects the more highly organized: everything beyond the horizon of such a type as *Nemalion* is cut off abruptly, with apparently no possible trace of any preceding phyletic stages, in which the peculiar spermatogamy and the life-cycle of the Florideae must have been evolved. The Bangiaceae possibly bear about the same relation to the Florideae that the Ulvaceae may to the Siphoneae: *Chara* stands, with its associated types, so absolutely alone, as a relic of parenchymatous corticated Chlorophyceae, that since the time of Hofmeister it has been more or less associated with Archegoniatae, by every possible mode of distortion of its peculiar features. The Phaeophyceae can show nothing more elementary than *Ectocarpus*, in which all the special characters of Phaeosporean filamentous phytobenthon are in full operation; all minor forms appear as decadent rather than more primitive types, though often regarded as transitional to 'Brown Flagellates', even of fresh-water ponds.[2]

The sea contains the relics of an assemblage of many races, without indication of their beginnings, and without discernible future; just as a tropical forest may contain relics and vestiges of indefinite 'natural orders' of Flowering Plants; and while this standpoint applies more particularly to the present consideration of Marine Phytobenthon and its higher derivatives, it becomes even more insistent in the vestiges of still older plankton-groups. It is, for example, extremely difficult to find any adequate appreciation of the possible mode of evolution of a Diatom.

While it thus remains a matter of purely idle speculation to attempt to link up at this distance of time the few survivors of the lost races, it is possible to trace *analogies in the solution of similar biological problems*, though this may afford no criterion of direct affinity; and the closer the parallelism in the problem, the closer may be the solution: accepted estimates of 'affinity' may be often nothing more than such parallelism in the solution of some vaguely understood physiological problem.[3] The progression of evolution is to be

[1] For reef-building calcified Algae of the Lower Carboniferous, recognizably the same class of vegetation, though not necessarily Floridean, cf. Garwood (1912), Quart. Journ. Geolog., pp. 459, 584, *Solenopora*.

[2] Cf. *Phaeothamnion* of German Lakes, *Phaeodermatium* and *Phaeococcus* of damp earth: Blackman (1900), Ann. Bot. xiv, p. 685; Cavers (1913), New Phyt., p. 122; following Scherffel (1900), W. M. Kiel, iv, p. 21.

[3] After all, the highest ideal of botany is not the demonstration of 'affinity', any more than to 'classify'; but to deduce the problems of plant-organism, and the

interpreted, not so much as the actual modification of organism in direct line of descent, as a progression of new problems, solved in succession by advancing organism, of often different though associated origin: modern classification of individual genera and families is often but the expression of some common biological horizon; and such classification by general '*physiological resemblances*' is really no more a picture of the exact mode of evolution and relationship than the older method of classification by general *morphological resemblances* ('affinities').

Thus it may be the present fashion to link all algal types on to Flagellates; but this is only another way of expressing the fact that all come equally from plankton organisms which had similarly solved the problem of vertical ascent by a contractile motor organ,—the only solution possible given the attainment of a 'contractile' superficial zone of cytoplasm, and soon expressed in limiting terms. That higher-grade phytobenthon is derived from such phytoplankton is obvious; there is nothing else for it to come from; but the distinction between phyla of 'green', 'red', and 'brown' algae, as traced in fundamental differences in cell-metabolism, may be even older than the flagellated phase. All elementary organism was necessarily autotrophic, and it is freely admitted that all animal organism has been derived from flagellated Protista; but behind the flagellated phase there must have been still simpler organism, aflagellate and passive; and this again must have been predominantly *autotrophic* also, and so conceivably of 'plant'-nature.[1]

While problems of phyletic origin are not to be solved by any empirical linking of generic types in more or less picturesque 'trees', and adjusting and balancing the forms at requisite levels in the manner of the 'cross-affinities' of the morphologists of the nineteenth century,[2] the rise of a new race represents a sequence of biological stages constituting the solution of new problems as they arise, one by one, or often more or less simultaneously; and the mechanism can be only recalled by reconstructing the steps of the progression, in such a manner that the machine will work on lines intelligible to botanists, from the consideration of the mode of operation of plant-life as a whole at the present day.

A good example of this correct mode of approach is afforded in the spectacle described by Bower ('Land Flora', p. 142) of the 'spindle-shaped embryo' sterilizing itself, and putting out 'enations', while parasitic on the gametophyte

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methods in which they have been solved. It is not the degree of consanguinity of Mr. Jones and Mr. Smith which is of interest to thinking people, so much as their outlook on their special life-problems.

[1] Zoologists have tended to calmly assume that 'animals', i.e. proteid-consuming organism, were first evolved (Lankester, Enc. Brit. ix. edit. 'Protozoa', and 'Text-book of Zoology' (1909), p. xv; Minchin (1915), 'Evolution of the cell', Brit. Ass. Rep. p. 437; 'Text-book of Protozoa' (1912), p. 245) and that some of these were converted into plants by the evolution of chlorophyll, and the formation of a rigid wall (!). But to invent a machine that will continue to elaborate proteid is to evolve quite high-grade life; and this is what has apparently been done in the sea. Taking the autotrophic flagellate as nearest the original stock of the Protista, it would appear that dominantly holozoic flagellate phyla diverged subsequent to the evolution of chloroplasts; as again suggested by the relation of our eye-perception of 'light', to the Protozoan eye-stigma, originally a part of a chloroplast. (Cf. Doflein (1916), 'Protozoenkunde', p. 398.)

[2] Hooker (1873), 'the protagonist of evolution', was less clear in the precise details of his own subject (cf. 'Le Maout and Decaisne', p. 994, on 'Cross Affinities'): 'The cohorts may be fancifully likened to the particular beads of a necklace, the beads touching at similarly coloured points of their surfaces . . . such colours representing the "cross-affinities" which the cohorts display with others remote from the position they occupy.'

generation; and the working hypothesis of the 'Land-Flora' is justified according as it succeeds in illuminating the still very obscure phases of such apparently fantastic and crude assumptions. The point remains,—*Why did it?*

Since the time of Hofmeister, the 'Landward Migration' has been considered almost exclusively from the standpoint of the newer subaerial modes of reproduction; whether as expressed by the special type of the female organ (the Archegonium), or in the form of wind-borne spores liberated by the dehiscence of a novel 'sporangium' (Pteridophyta), or 'sporogonium' (Bryophyta). Traces of these organs have been sought in *Chara* (Hofmeister, Goebel), and in other Pond-types (as in *Coleochaete* and *Oedogonium*), with scanty success: all the more elementary phases of Land Flora progression being apparently 'cut off' as rigorously as those of Marine Benthon. Hence there is no need to wonder that there is no trace of an archegonium or 'archegoniate alga' in the sea. This hypothetical plant probably never materialized: there is no trace of evidence or suggestion that an archegonium ever existed in a permanently submerged condition. Even the evolution of the archegonium requires to be approached on broader lines: after all, the first point is rather,—What is an archegonium, and what problems was it originally designed to meet? That it was a remarkably successful solution of some biological problem is certainly shown by its dominance, and persistence in a recognizable condition, long after it has ceased to be essential to the mechanism of fertilization (Gymnosperms).

Conclusions.

(1) A landward migration of plants *via* estuarine conditions of fresh-water, involving diminished proteid-metabolism owing to lack of food-salts, is less possible, as tending to reduce the output of reproductive cells below the previous margin of safety, and cannot be reasonably postulated. Direct migration from the sea to dry land or occupied ground is an even more remote possibility.

(2) Surviving races, being but the stray relics of mass-variations, and the phases of transition becoming the more obscure as adaptation to subaerial conditions has been more successfully accomplished, evolutionary progression is to be regarded as a question of the elaboration of a general mechanism, rather than that of the collateral linkage of recent types.

(3) The discussion of any theory of 'migration' should be preceded by the examination of the possibilities of a mechanism of '*transition in situ*' (= transmigration).

III

THE ORIGIN OF THE ARCHEGONIUM

It may be granted that the archegonium, so long regarded as the distinctive attribute of the 'Archegoniatae', is clearly an end-product of oogamic evolution, the limiting term of something quite unknown, probably originating in something quite different from any recent archegonium, and, if we saw it, scarcely recognizable as such. Very probably again of polyphyletic origin, arising in phyla of marine algae of quite diverse descent, and convergent in general factors, as the limiting term of a special mechanism; at bottom no necessary guide to affinity, but merely indicating that the 'Archegoniatae'

may be the expression of a number of phyla at the same physiological horizon in this particular respect.[1]

The distinctive value of the structure, regarded simply as a means of obtaining fertilization *in situ*, for an oosphere in which post-sexual nutrition involves a parasitic diploid embryo, merely expresses an economic mode of reproduction which has been in full operation in all the phyla of the Florideae as far back as they are known, and leading equally to a decadent deteriorated phase ('Sporophyte'),[2] the more decadent as the more efficiently parasitic (Florideae, Marchantiaceae). Such phenomena are part of the plant-equipment evolved in the sea; hence it was not solely to these functions that the archegonium owes its special morphological attributes: its origin must be sought in the transmigrant phyla, as the result of the transition to the new environment. One fact, however, stands out as essentially significant. In no case does the oosphere fertilized within an archegonium become a resting-spore, with a cuticularized wall. 'Germination' is direct; or rather,—since the term germination is wrong and objectionable, being borrowed from the consideration of the perennating seed-stage of Land-Flora,—growth continues without a perennation-phase. This is the fundamental characteristic of marine phytobenthon, and is the point which clearly delimits the migrant *Chara* from any connexion with the main progression. From this fact it may be reasonably assumed that fertilization *in situ* obtained in the sea before the period of transmigration set in, and the oospheres of the 'proto-Archegoniate' were no longer discharged in the open medium. As the Florideae had long since passed through this condition in the remote past, the fact that no other marine algae (Phaeophyceae, Chlorophyceae) attain to it implies no objection: and conversely, if fertilization *in situ* had been attained after the transmigration, this stage would have been utilized as a 'resting-stage,' as has been done in such types as *Vaucheria*, *Spirogyra*, *Oedogonium*, *Coleochaete*, and *Chara*, all fresh-water transmigrants; though *Vaucheria* may still persist on estuarine and tidal mud.

As a multicellular structure produced by the segmentation of cell-units (multiseptation), it is sufficiently clear that the archegonium is a derivative only of a truly parenchymatous type of soma; it is not a mere filamentous 'trichome'-derivative, but a *member* of minor degree, and hence of the morphological value of a small lateral ramulus (gametophore).

(1) Small lateral ramuli devoted to reproductive purposes are general among the Florideae; as in the stichidia of *Dasya*, and the minute cystocarpic ramuli of *Delesseria sanguinea*, *Sphaerococcus*, as also in *Calliblepharis*, *Callophyllis*, and *Epymenia* among more substantial sub-parenchymatous forms: though the Florideae are never of truly parenchymatous organization.

(2) Among the corticated Characeae both the antheridial receptacle and the oogonial system are clearly highly specialized 'ultimate ramuli' of originally very similar organization.

(3) Again in the Phaeophyceae, simple multiseptate ramuli were established in the Ectocarpoid series as plurilocular gametangia, and the type is curiously persistent among Phaeosporeae to *Cutleria*. The analogy of an archegonium

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[1] For example the somatic organization of the thallus which gave rise to Bryophyta, with rhizoid attachment only, was much inferior to that producing the Pteridophyta with 'roots' derived from lateral ramuli as crampon-systems. The Bryophyta, Filicineae, and Lycopodineae retain distinctive vestigial flagellated phases in their antherozoids.

[2] Normally diploid, though in several cases reduced to a haploid phase, apparently secondarily as in *Nemalion*, *Scinaia*, and probably in *Batrachospermum*, *Chantransia*, etc., with decadence of tetrasporangia to monosporangia.

with such a 'plurilocular' organ was considered by B. M. Davis (1903) with very imperfect data; and little progress seems possible along these lines.[1]

It is interesting to note that in the only Moss fairly comparable in organization with high-grade Algae, *Sphagnum*, the archegonium presents traces of a more massive branch structure.[2]

Treated on broader lines, deduced from the study of the sexual organs of heterogamous algae, and the asexual organs of Heterosporous Pteridophyta, it may be fairly accepted that the specialized 'mega'-organ is always the adapted limiting term of a series associated with a concentration of food-supplies in one surviving reproductive unit; and that the original state of the organ from which it started, as also the original condition of the reproductive unit, is more likely to be traced in the 'micro'-organ: the antherozoid and the microspore being generally accepted as the typical representatives of their respective morphological order; and it is thus on the *Antheridium* of the Archegoniatae, rather than on the archegonium itself, that investigations should be based. This at least seems sure ground: if we can find the homologue of the antheridium of the Bryophyta in marine algae, the archegonium should necessarily follow.[3] Divested of the 'neck' which appears as a secondary extension of an original distal dehiscence-mechanism, the archegonium reduces to a simple cellular organ of wall (venter), contents, stalk-portion, and dehiscence-mechanism. The 'contents' a single mother-cell, giving by one mitosis an oosphere and a vestigial 'ventral-canal cell', is clearly a limiting expression of many ultimate mother-cells producing by several acts of mitosis a number of gametes, the last units being thus paired, and not necessarily separated by a septum.[4] The antheridium reduces to the same simple factors, as a body with stalk (a relic of the original undifferentiated branch-region), and a reproductive region differentiated as a 'wall' and 'spermatocyte-tissue', together with a necessary dehiscence-mechanism. Increased volume due to intercalary growth, more abundant spermatocyte-tissue, growth by an apical-cell (Musci), and specialized cylindrical form (*Polytrichum*), do not add anything to the essential features; but in fact repeat normal branch-factors. In the alga-like *Sphagnum*, it is interesting to note the longer stalk, the more spherical form, the identity of position as a branch of the stem-system, identity of morphology, as being replaceable by a vegetative bud, the perfect maintenance of the factors of an 'ultimate ramulus' with special growth,[5] and even its so-called 'axillary' nature. The antheridium of a Fern presents the same factors on a reduced scale; and a similar organization still further reduced and 'immersed' may still be traced vaguely in the more decadent soma of *Anthoceros* and of *Ophioglossum* (gametophytes). In all these organs three factors are involved which do not obtain in any type of the Phaeosporeae or Florideae; e.g.

(1) The differentiation of a septate wall.
(2) The massive spermatocyte-tissue.
(3) The apical dehiscence-mechanism.

In one type only of the Phaeophyceae, the Dictyotaceae, however, the

[1] B. M. Davis (1903), Ann. of Bot. xvii, p. 477, 'Origin of the Archegonium'.
[2] Cf. Cavers, New. Phyt. (1911) p. 44.
[3] This attitude was correctly taken up by B. M. Davis (1903), loc. cit.
[4] A septum, as a definite cellulose membrane, being merely the expression of the deposit of polysaccharide debris of proteid-metabolism, is naturally wanting where such metabolism is inhibited by the isolation of a truly sexual cell.

The occurrence of two functional oospheres as an occasional 'monstrosity' is so readily intelligible that it excites little enthusiasm.
[5] Cavers, New. Phyt. (1911) p. 12.

segmentation of the multilocular gametangium is continued to definite spermatocyte-tissue, as a mass eight units in extent each way.[1] On the other hand, alone of all Algae, a distinct *analogy* in biological mechanism is traced in *Chara* for the other two factors, in which a mechanism of very similar 'antheridial' appearance, with practicable wall, dehiscence-mechanism, and packed masses of 'antheridial filaments' clearly exhibit these biological factors; though so obviously different in the mode of anatomical expression, and in a distinct type of organism that has no known history. It may be at once inferred that *Chara* must have met the same environmental problems, and solved them in a very similar manner, though in different terms. *Dictyota* may have a suggestive initial stage, but *Chara* outlines the Proto-Archegoniate; that is to say, the last two types must have passed through a common experience. The fact that *Chara* has a 'resting zygote', adapted to withstand considerable desiccation, is sufficiently suggestive of the fact that a change to conditions of subaerial environment was the determining factor in common; and that *Chara* has attempted the same transition without much success,[3] while early Archegoniatae solved the problem. In this respect *Chara* is not to be regarded as a Proto-Archegoniate, so much as a Pseudo-Archegoniate. It cannot be in any Archegoniate series with only one generation in the life-cycle.

Taking this remarkable analogy of *Chara*, the transmigrant failure, as a clue, the significance of these special biological factors may be determined as:—

(*a*) The separation of a protective wall of aqueous (and also photosynthetic) cells, with a minimum of one layer.

(*b*) A mass-condensation of spermatocyte-tissue in minimum space, and hence approximately of spherical form (cf. *Sphagnum*); effected in *Chara* by a packed mass of simple 'trichome' filaments.

(*c*) A dehiscence-mechanism in terms of living-cells, by osmotic dilatation, or by mere swelling of residual mucilage; adapted for dehiscence under water, or in saturated atmosphere, and liberating flagellated zoïds.

(*d*) The zoïds have lost their chloroplasts and eye-spots, and thus become relegated to the status of true 'sexual-cells'.

(*e*) In all early fresh-water phyla (*Pellia*, *Sphagnum*, *Marchantia*, *Chara*) the motor power of the flagellated zoïd is conspicuously increased, as indicative of special adaptation to a medium no longer in movement (standing pools), and the whole work of translocation must be done by the zoïd itself.

Of these special factors, found in no modern wholly marine type, just as no resting-spore with perennation-mechanism of exosporium occurs in normal marine benthon,—though present and associated with a perennating zygote in *Chara*, not so much an estuarine plant (as *Vaucheria*) as a product of lagoons of the sea-margin,—the biological interpretation is clearly that of a means of protection against desiccation during early stages of maturation, while exposed to a sub-saturated atmosphere; becoming effective with dehiscence in the adult stage on access to the fluid medium; quite as much as the expression of problems of gas and food-supply to non-autotrophic zoïds. Whether the last factors be of primary or secondary importance, they cannot be neglected; and it is evident that in such a mass-aggregation the

[1] L. Williams (1904), Ann. Bot., p. 189.

[2] Cf. B. M. Davis (1903), loc. cit., p. 491.

[3] 'Characeae', cf Migula (1897). *Chara fragilis* vegetates among grass on wet ground; *Nitella mucronata* was found growing self-supported 10 inches high, in a special case of damp air (Migula, p. 158).

internal zoïds are supplied with food and oxygen among their fellows; and since none are now in immediate contact with the external medium, all such nutrition must be indirect, and the wall-units may play an important part in nutrition as well as mere 'protection', which really reduces to a question of water-supply.

Such a structure has obviously no relation whatever in fundamental organization to the general case of the plurilocular gametangium of the Phaeosporeae, in which every zoïd is autotrophic, and has its own frontage to the medium. But the case of *Dictyota* shows that this condition may be initiated in correlation with advancing oogamy in the case of an algal family of the warmer seas. From such a gametangium the case of the Bryophyte antheridium wants little but the localization of a protective wall-layer, and a consequent dehiscence-mechanism to let the zoïds escape. *Chara*, which illustrates the attainment of the same adaptations, is a transmigrant type, and the special factors are the expression of the earlier stages of a secondary transition to subaerial environment; that is to say, such organs will bear exposure to sub-saturated air, and will liberate active zoïds on chance wetting, as in the case of the Moss-antheridium of the present day. This is the more clearly recognized on simply growing *Chara* under a bell-jar over water; the shoots rising 2–3 inches out of the water, and the erect ramuli forming close bud-structures. The relation of the very definite terminal buds of *Chara* to the position of the oogonia on the protected anterior margins of the lateral ramuli, and the development of specially protected reproductive organs on subaerial shoots, confirms the view that these systems are essentially subaerial in origin.

An analogous attainment of the same biological factors is equally well-expressed in the oogonial system of *Chara* and in the archegonium of the Moss; this in fact is why they have been often considered allied. One explains the other, and both are explained by the more 'primitive' (generalized) micro-gametophore. The oogonium itself is essentially a multiseptate ramulus (much reduced in *Chara*, to a limit of 2–3 cells, including the basal node-cell); but the protective function of a 'wall' is transferred from the vestigial somatic units ('Wendungszellen' of *Nitella*) to efficient corticating ramuli, also reduced to a minimum of 2–3 units each. The mega-gametes are reduced to a single huge oosphere (averaging 400 μ. diam., and larger than anything in Phaeophyceae or Florideae); while the 'dehiscence-mechanism' is also provided by the corticating ramuli ('corona'), with a general resemblance to a 'neck', in construction nothing whatever like one, though sufficiently deceptive to early observers. On the other hand, the oogonium of *Dictyota* shows no signs of such modification, being cut down to the minimum of one oosphere from the first: that is to say, the archegonium mechanism must have started at a phase of heterogamy earlier than that now presented in *Dictyota*, though the oosphere of the latter is still freely discharged.

In the case of the Bryophyte archegonium, the surviving oosphere is protected from desiccation by the parenchymatous venter, which may be more than one cell thick; and when matured, the apex of the neck dehisces in chance-supply of external water, and allows fertilization *in situ*; the length of the neck suggesting a 'chimney-device' for economy of the chemotactic material.

The fact that the exaggerated elongation of the chimney-device (*Marchantia*) is to be regarded as a later xerophytic adaptation for continued exposure of the adult organ in sub-saturated air, is rendered probable by the utilization of a similar device in pollination-mechanisms, as in the original integumentation of the ovule, the exaggerated pseudo-stylar tube of *Welwitschia*, and the true stylar canal of Angiosperms.

As in the more generalized antheridium, the new departures are factors

implying subaerial transition, the outcome of new conditions, and hence never present in the original purely aquatic (marine) phase. A plant presenting them may be classed, as in the case of *Chara*, as a migrant, but perhaps preferably as a transition-phase (*transmigrant*) expressing passive endurance of the change *in situ*. Morphologically *Chara* is a very elementary algal type of corticated parenchymatous organization, inferior to many marine algae, even on the horizon of the archaic *Desmarestia;* biologically it is a semi-transmigrant; the adapted sexual organs readily falling back to a condition of constant submersion, in which the special protective adaptations are largely meaningless. Confirmatory evidence of the transition phase is observed in the perennating zygote; but it has no other relation to the Bryophyta, beyond the presentation of the onset of similar biological factors: the oogonium has nothing in common with an archegonium, nor would it ever become 'archegoniate' on carrying the new departures to further stages; while the complete divergence of the type, on lines entirely different from those of higher land-flora, is seen in the fact that the Characeae are wholly destitute of an asexual diploid phase in the life-cycle.

The conclusion that the Characeae, alone of Green Algae, remain to demonstrate the meaning of the mechanism of transition in the reproductive organs, supplying factors directly analogous, though so different in detail and phylogeny to those of the antheridia and archegonia of Bryophyta and Pteridophyta, is curiously correlated with the evidence that *Chara* may be a direct migrant from the sea, with representatives still living in brackish parts of the sea and salterns; and one species (*C. baltica*) is still obligate in salt water, though the majority of forms are largely estuarine and pond-weeds. This lends additional support to the view that land-flora was evolved directly, by partial emergence, from salt water, in which normal marine nutrition continued unaffected for some time after the reproductive organs, exposed at the ends of the shoots, had begun to be adapted to new conditions of partial exposure to sub-saturated air. Thus instead of postulating an estuarine migration under starved conditions of nutrition in fresh-water, while the reproductive organs remained unaffected as those of a hypothetical 'archegoniate alga', the preliminary stages of land-migration were just the reverse, being undoubtedly initiated in the environment of salt-water, with full autotrophic nutrition, while the reproductive mechanism was the first to be adapted to the new conditions, as the chances of wastage became the more rather than less pronounced. That is to say, the reproductive organs were first successfully adapted, while the older methods of nutrition in the original food-solution remained at their full strength; and reproductive output being efficiently maintained, the race continued to survive. *Chara*, it is true, suggests several points as analogous and parallel modifications; but it remains a failure. We know from the result that the successful transition was effected by an alga with a diploid phase, in which the post-sexual nutrition of the Florideae had probably already followed fertilization *in situ*.

Thus the archegonium cannot be regarded as a mechanism initiated solely to secure chemotactic fertilization *in situ;* this can be done quite as effectively in *Chara* by a different mechanism. As an organ economically producing one oosphere, it is again no better than the oogonium of *Chara* or the carpogonium of the Florideae: nor was it intended solely for the post-sexual nutrition of a diploid zygote; this had been done in much simpler fashion by all the Florideae. But it may combine all these three functions secondarily; as *Chara* does the first two, and the Florideae the last two; and even so far it is an improvement on both; while its essential features were the result of response to subaerial exposure.

Similar biological equipment is common to both male and female organs, and it is impossible to say at what stage of either incipient or reduced oogamy it may have been initiated; since reduced oogonia present much the same appearance as incipient ones by the omission of the food-storage.

Although not much to look at, and subject as we know it in Land-Flora to ultimate phases of deterioration and decadence, the archegonium is really, as its universality in Land-Flora would suggest, a perfect triumph of minimum mechanism, successfully subserving many functions; undoubtedly polyphyletic in Bryophyta and in Pteridophyta, but contemporaneous in origin, and the expression of biological adaptation in the specialized ramuli of a parenchymatous soma of marine algae, on a horizon comparable in some respects with shrubby Fucoids with rhizoidal or crampon attachment-organs; in others with Florideae in which oogamy has been superseded by post-sexual nutrition and a consequent parasitic diploid phase; again curiously following *Dictyota* in the parenchymatous spermatocyte-tissue which gives the initial possibility of the structure.

The idea begins to emerge that when the first land gradually lifted above the primal sea, bearing all forms of marine life on it, the successful transmigrant algae of the first land-migration combined the best and highest factors of marine equipment, as illustrated at present in many divergent surviving groups, but were not definitely like any known single type. More rudimentary filamentous benthic forms may have persisted as the phytobenthon of fresh-water in a condition of further deterioration; saprophytic and parasitic deteriorants living on dead associates may have survived as Fungus-phyla, just as many more or less holophytic plankton-flagellates (including Diatoms and Peridines) survive in fresh-water ponds, practically unaltered except for their perennation-phases; but the Prototypes of the Archegoniate series were probably the best the sea could offer at that or any other time, and it is from the best of modern marine algae that their characters are to be deduced. The inexplicable fact remains that they appear to have been a green, starch-forming series of parenchymatous organization, a type at the present time wholly unrepresented in normal sea-water; the few genera of the Characeae being the only relic of the types with these somatic characters.[1]

[1] The most conspicuous failure of the systematy of even 'modern botany' has been the confusion of the structural details of physiological organs (ovaries, seeds, &c.), with indications of actual 'affinity'. Homoplasy and 'convergence' have been much neglected; and though this may have been excusable in the case of older generations, seeking for a sign in the entire absence of any definite orientation, there is no reason for the retention of such conceptions in the present day. Possibly in no case is this idea more deeply rooted than in the obsession that the 'Archegoniatae', once they have been distinguished by such a striking and convenient name, are necessarily a coherent group, or monophyletic, and hence dating back to some wholly hypothetical 'archegoniate alga'. It cannot be too clearly stated that the archegonium, as a specialized reproductive multicellular ramulus, is eminently polyphyletic; and is approximated, by convergence to the limiting condition of a single included oosphere, in many phyla still conveniently included as 'Vascular Cryptogams' and Bryophyta, which date back without doubt, quite independently, to the flagellated plankton-phase; as indicated by the wholly distinct type of flagellation retained by the motile antherozoids of, for example, *Sphagnum* and *Pellia*, the Filicineae (*Aspidium*), the Lycopodineae (Selaginella), and even the case of *Isoëtes*; quite apart from any necessary connexion with the ancestral stages of Angiosperms. The elaboration of the Archegonium, in which the isolation of a peripheral series of 'sterile' units has been elegantly distinguished as 'encapsulation' (Bower, 1919, p. 488), is no more peculiar to the archegonium; than to the antheridium with sterile 'wall'-units, or, as will be seen later,

Conclusions.

(1) The archegonium was polyphyletic in origin in marine environment as a minimum mechanism, and never existed in a condition of completely submerged algal benthon.

(2) The organization common to both antheridium and archegonium in Land-Flora is to be regarded as the effect of the response to subaerial conditions in the reproductive organs of marine algae, of which tropical Dictyotaceae alone suggest the initial stage.

(3) The evolution of Land-Flora was a phase of transition *in situ*, rather than involving a preliminary landward 'migration' *via* fresh-water; the biological factors being exposure to more or less desiccation, and the removal of the food-solution.

(4) In the commencement of the process there is little that is really new: the Proto-Archegoniatae may combine characters which are known to have been the product of marine existence as phytobenthon; but the preceding equipment of the sea is utilized in the transmigrant organism; such factors are adapted, and not invented *de novo* a second time.

IV

THE POSSIBILITY OF DIRECT PROGRESSION FROM THE SEA

In dealing with the initiation of an entirely new sub-kingdom of vegetable organism, the first step is to get beyond the mere parochial outlook of 'Pond-life', and to take broader views of the problems involved. The whole world is the field of operations, and considerations must be based on at least a continental scale. Thus the evolution of *phytoplankton* is to be considered from the standpoint of a present sea-area of at least $\frac{2}{3}$ of the world surface, and originally more probably the whole of it; with a mass of water averaging two miles or more in depth, in which autotrophic life is not likely to have penetrated more than 100 fathoms from the surface; beyond this epoch the

to the spore-capsule (sporogonium) of the Hepatic, and the sporangia of Pteridophyta. *All such reproductive organs of multiseptate 'parenchymatous' plants are themselves morphologically derived from multicellular (multiseptate) ramuli.* The same evolution of a protective 'epidermal' layer is common to all, as a factor in the solution of the problems of transmigration. There is no need to look for an 'archegoniate alga'; a multicellular alga, with multicellular ramuli set apart for reproductive functions is all that is necessary (cf. 'stichidia' of Florideae). The problem of the phylogeny of the transmigrants is again by no means restricted to the demonstration of the origin of the archegonium, however much this may obsess the student of the 'Archegoniatae'; the archegonium is after all but a trivial matter. The whole point of the evolution of the land-plant is based on the retention of the differentiated 'sexual' mechanism of the aqueous and benthic phase practically unaffected, while a somatic organization is being perfected for subaerial conditions. The real problem of the transmigration is one of immediate nutrition, and concerns the mode by which an autotrophic plant, built for living in an aqueous food-solution, can be converted into one equally successful in an atmospheric medium, with no external food-solution beyond that in which the base of the plant may be still more or less immersed. The 'encapsulation of the oosphere' is a detail; and massive reproductive ramuli are part of the equipment of the higher-grade massive algae of the sea, though they may appear a novelty to those who are only familiar with the starved transmigrant types of fresh-water

first stages of marine phytobenthon may be considered, not from the modern standpoint of mere rocky fringes, but of the uprising of undulating continental land-masses to within a range of 100–50 fathoms, at a moderate rate of something like a foot in 100, or even 1000, years. With all subsequent rise the amount and extent of benthic progression would be increased, until the rocky masses break above the surface of the water as the first 'dry land'; and marine phytobenthon culminates in the sub-littoral zone of the upper 10 fathoms or so around the fringe of the land-masses; spreading out over vast areas in shallower seas as submarine forests, the distribution of which is still little known, because they cannot be seen, and are with difficulty explored or even surveyed. The floating masses of the Sargasso Sea of the North Atlantic, over a vague area of possibly 250,000 square miles, affords a suggestive idea of the extension of marine vegetation beyond the horizon of the plant-life of our narrow seas.

Similarly the passage from marine phytobenthon to subaerial environment may be based on a continual progression of the same factors, operating over continental areas where the land remains fairly flat and undisturbed by minor foldings, as for example in the continental land-mass of Northern Africa. Consider the case of such a region brought to the sea-level, teeming with life, under a vertical sun, the water gradually disappearing, but subject to changes of level under the influence of a shallow oceanic tide. So long as the water remains in connexion with the open sea, the influence of the bi-diurnal tide would continue to be felt, if only to the extent of 1–2 ft., and the exaggeration of such motion by wind-action on the surface would be always liable to produce a more violent movement of the medium than small plants of 1–2 ft. would be able to withstand. This may be compensated by the breaking up of the area into discontinuous pools, and the partial emergence of the more massive growths. A greater objection to such direct transmigration from sea-water follows from the consideration of such pool-areas, which under the ordinary intense insolation of a tropical sun would tend to rapidly concentrate beyond the osmotic capacity of plant-organism; and in the tide-pools of a tropical reef the sea-weed vegetation often 'deteriorates' far more rapidly than in Northern Seas. But before eliminating the possibility of such direct adaptation from the normal conditions of the sea, and falling back on estuarine migration to fresh-water as a last resource, it may be pointed out that all objectionable influences of intense insolation, of desiccation by combined effects of wind and sun, as also the injurious concentration of the medium, may be ameliorated, or even eliminated, by the maintenance of a sub-saturated atmosphere, and a sky of fog and cloud with tendency to atmospheric precipitations. It is in fact the prevalence of such conditions that renders possible the algal migration to the Salt Marshes of Northern Latitudes, for which a few pleasant summer months are by no means typical of the annual period as a whole. The same applies to the steaming conditions of a tropical Mangrove Swamp, in which fishes (as *Periophthalmus*) may run about on their fins and catch land-insects, or even climb on to the trees.

Again, speaking generally, the problems of plant-life may be arranged in order of priority as concerning; firstly, the life of the individual as expressed in phenomena of nutrition; and secondly, the continuation and growth of the race, as expressed in phenomena of propagation and reproduction. The life of the individual is based on food-supply, as involved in its relation to water and food-salts, and its capacity for photosynthesis; but even beyond this on the initial source of energy, as expressed in solar radiation and the normal katabolic processes of aerobic organism utilizing free oxygen over the hours of darkness. The problems to be considered for migrant or transmigrant algae, presuming the necessary exposure to sunlight are thus:—

(1) Oxygen-supply; (2) Food-salts; (3) Water-supply; (4) Reproduction (sexual and asexual).

I. The question of oxygen-supply presents no difficulty. A transfer from a medium, in which at best the oxygen-content is never more than 0·8 % of the volume, and more generally averaging about 0·5 %;—this supply being precarious in competition with aerobic bacteria and animal organism, with dependence for more on photosynthesis which is only available for at most half the total time, with little provision for storage,—to a medium with at present a constant supply of over 20 % of the gas by volume, is so marked an improvement, of almost intoxicating value, that there can be no doubt that, other things being equal, this factor alone provides a primary reason for the successful migration of plant and animal phyla alike from the original environment of the sea. As organisms sensitive to a variation of 1–2 % from the normal, we are ourselves not in a position to grasp the meaning of such a change. Practically the same applies to the change from a medium, in which the light-supply is necessarily poor and subject to further reduction, to the brilliance of open sunlight. The available sources of working energy are thus enormously increased to any plant-organism which can emerge above the surface.

II. The problem of water-supply, merely as water, is solved at once by the hypothesis of a sub-saturated atmosphere; and may be also approached from the standpoint of (1) a primary existence within the region of the splash of sea-water, (2) the effect of copious atmospheric precipitation, and (3) the gradual initiation and utilization of an absorptive mechanism, as the preceding diminish in effectiveness. Exactly the same difficulties obtain in the consideration of the evolution of land-plants from hypothetical conditions of fresh-water; even if not in greater degree, owing to the elimination of the 'region of the splash' in more quiet expanses. Thus massive growths of Phaeophycean thallus, as *Ascophyllum* of British Seas, withstands, and even requires, an exposure to air of just half its total time. *Pelvetia* at the high-tide line possibly exists with a percentage of only 5–10 % of total submersion; withstanding desiccation the rest of its time by the prevailing dampness of its environment, at the margin of the splash of the waves. On rocky less-exposed coast of the Faeroe Islands, *Pelvetia* will exist 15 ft. above the tide-mark (Börgesen), while on more exposed coast dwarf *Fucus spiralis* (= *platycarpus*) may extend 20–35 ft. above high-water level. Among the Chlorophyceae, *Chara foetida*, as a parenchymatous corticated type, grows on turfy moors, only partially submerged, in tufts and masses creeping among the grass roots; while *Nitella mucronata* has been found growing in dark sheltered crannies of falling streams, erect and flourishing for a height of 10 inches, with no other mechanical assistance than the turgidity of its non-corticated axial cells (Migula). Similarly in damp tropical environment species of *Catenella*, *Bostrychia*, and *Caloglossa* (Florideae), may more or less emerge from the water, and live among grass, mosses, and herbage of the swamp and river-banks, as also on stems of *Nipa* and roots of mangroves. Hence mere water-supply, as H_2O, presents little difficulty to even delicate algal vegetation, any more than to *Vaucheria* on a damp flower-pot, so long as a sub-saturated atmosphere is available. Beyond the small amount required for new anabolic growth-processes, water is only required to make good the wastage of desiccation. Even to-day the extreme difficulty of drying Fucoids in the damp air of wet winter months is the fundamental problem of the kelp industry.

III. A much more important consideration is that of food-supply: presuming normal photosynthesis of carbohydrate, the further progress of

proteid-synthesis requires a readily available supply of Nitrogen and Phosphorus ions, as well as more widely distributed compounds of Calcium, Potassium, Magnesium, and Sulphur; and this becomes a much more critical factor in plant-migration. Thus, taking as an example the case of the exposure of a *Laminaria* or even *Lessonia*-forest in a saturated atmosphere, at low tide for an hour or two; the plants remain erect with no apparent injury, and will not suffer any harm so long as the atmosphere remains subsaturated, though the large laminae may droop owing to lack of support from their flotation-mechanism; but even this would not be noticed in stouter more substantial growths of such forms as *Cystoseira ericoides*. Though the water-problem may be satisfactorily adjusted, it is evident that the plants would ultimately die for want of (1) food-salts, in the absence of an absorbing mechanism in the basal part of the plant still in the water (hapteron-system), and (2) a conduction-mechanism in the main axis. The same applies to the dwarf vegetation of the upper tide-range, removed from the food-solution for more than half their life-period; all such forms, as also those of the supra-littoral zone, can only exist as mere starved organisms, in which with no excess proteid-synthesis the production of reproductive units may be wholly suppressed, as in the similarly exposed and starved brown sea-weeds of the salt-marsh. It is thus from the standpoint of food-salt supply that any transmigration, to be effectual, demands the initiation of a basal absorptive mechanism, and the initiation of an upward direction of conduction in the axis: the water-problem may be at first quite immaterial. In modern marine phytobenthon the only definite conduction in operation is traced as a slight descending current ('descending drift') in order to provide for the nutrition and growth of the more shaded hapteron-region; this being only exaggerated to a definite system of food-conduction in the case of such massive exposed types as *Alaria*, *Saccorhiza*, and *Macrocystis*, in which the reproductive organs are borne on the more sheltered basal portions of the plant; in such case an existing current would require to be reversed.

It is to the somatic organization of the new phyla that attention must be paid at first; no racial improvement is possible until the individuals have the mechanism of their everyday existence established on a satisfactory basis; and problems of nutrition in the individual take precedence of those of reproduction as involving the existence of the race. Though many species and even genera among marine algae are maintained at present, and possibly have been so for indefinite ages, under conditions of vegetative growth and propagation alone, it is generally admitted that, for all higher types of organism, at least, the further improvement of the race is only effected through sexual reproduction; or, at any rate, the process is thereby so hastened that it becomes capable of discussion. So long as the output of reproductive cells makes good the wastage of the environment, the race survives; if it falls below a certain minimum the race vanishes, and need be no more considered. Reproductive efficiency may be presumed, while the race is progressing in its new environment, by the very fact of its existence; and in the case of such transmigrant algal forms, so long as any external source of water was present, the old story of flagellated isogamy, oogamy, or even spermatogamy of the Floridean type would tend to continue, unimpaired in essential mechanism, though probably progressively specializing along similar lines as restricted by time-factors. The actual facts of observation of the more elementary existing types of Land-Flora show that the transmigrant races all present advanced oogamy (a time-saving device), though retaining the flagellated antherozoid exactly as in *Chara*, and thus suggesting a transition involving the

environment of standing water, with the ultimate elimination of even tidal and stream factors.

Reviewing the possibilities of emergence, there can be in fact little doubt that the first translation from sea-water to sub-saturated air was deceptively easy,[1] and of immediate advantage in many respects; and, just as in the original assumption of the benthic habit by sessile flagellates of the plankton, it was only later that the difficulties of the transmigration became apparent and increasingly insistent, as the water-problems of land-vegetation (Xerophyton).

V

THE CULMINATION OF MARINE PHYTOBENTHON

IT remains to gather up the threads of the numerous and now widely disconnected types of Marine Phytobenthon, and to combine them into a more or less connected story of what probably took place in the transition-period which preceded the domination of the land by surviving types of Land-Flora. Consideration of the subject falls naturally under three headings:—

(1) *What were the possibilities?*
(2) *What probably happened?*
(3) *What have the survivors to tell?*

The last is obtained from the text-books of the present period; the subsequent history of the Bryophyta, Pteridophyta, and Phanerogamia, being so far the most critically explored branch of the science, over a period of fifty years (Hofmeister, 1851, to Bower, 1908). All further evolution of plant-life on the world is dominated by the necessity for economizing water-supply; and the conquest of the land by vegetation is based on the progressive capacity for nutrition and reproduction under conditions of still smaller and smaller supplies of this essential medium. But all progress is still limited by the consequences of the processes initiated in the older races; and all otherwise obscure, and at first sight wholly intelligible, phenomena of land-vegetation are to be traced back to their source in the environment of the sea, as the original equipment of earlier marine existence. The outstanding miracle of organization of a gigantic flowering tree-type of the present day is not in any sense the direct result of the response of autotrophic life to the conditions of environment on the land-surface, any more than a man represents the best possible mode of designing a heterotrophic mechanism for the same conditions: but both organisms owe the fundamentals of their construction to the fact that they are equally transmigrant from a preceding phase of marine

[1] The period of the transmigration covers an epoch during which autotrophic vegetation, originally built up as the response to the environment of *sea-water*, completely changed its conditions of life to become dependent on *rain-water*, of which enough falls at the present time to cover the whole world to a depth of about 3 ft. a year. Such a fundamental change, to be successful, must have been very gradual; and one is entitled to assume that the transition may have been inappreciable, partaking rather of the nature of a dilution of the medium; as the salt-content of the body-fluids of higher animals still resembles that of sea-water, though of a more diluted nature. To become successful, as modern land-flora evidences, such a transition-phase must have been, at any rate in its initial stages, not only tolerable, but distinctly advantageous: the difficulties followed later.

benthon, the course of which was established for all time in a still more remote condition of pelagic plankton.

What were the possibilities? The limitations of marine morphology and anatomy are now fairly clearly defined; and the fact emerges that it is in the highest degree probable, that at no time has any factor been evolved in the phase of marine benthon, which is not now illustrated by some still successful type of organism in the original habitat. The range of possibility in approximation to stem, leaf, and root-habit, elaboration of sexual organs, reproductive processes, and cytological phases of the life-cycle, are determined and scheduled, as the result of response over millions of ages of fairly uniform submerged environment. Nothing more need be expressed or postulated as data for the initiation of any new departures, and the 'Equipment of the Benthic Stage' affords the only starting-point conceivable for the 'Flora of Subaerial Environment', or that can be postulated. But though the various factors are now seen differently combined in different surviving phyla of Phaeophyceae, Chlorophyceae, and Florideae, in almost infinite kaleidoscopic variety, the same factors characterized the ancestral types from which 'Archegoniate' phyla have been derived; though they may have been combined in different degree, and the culminating types may have presented a greater range of their more advanced expressions than do individual algal forms existing at the present day: this affords in fact the clue to the reason why the latter are left behind. Thus, examples of the Florideae and Characeae persist as extreme cases in which a partial attainment of many high-grade features has not been associated with successful transition. *Chara* seems to have been handicapped by the want of a diploid phase to produce the wind-dispersed spores; the Florideae by inefficient cellular organization; the Phaeophyceae never attained fertilization *in situ*: the reasons for such apparent failure may be discussed under the special phyla.

Knowing the full range of factors available in marine phytobenthon at the present day, and admitting the vast antiquity of the group, and its probable constancy to the same conditions, ever since the transition to Land-Flora took place, it should be possible by the subtraction of such factors from the vital complex of the more elementary types of land-vegetation, to deduce the residual factors of subaerial specialization; a method that has been already attempted in the case of the Characeae. *For example;* there is on hand, as the general sum of benthic equipment in existing marine types:—

(1) The possibility of a massive parenchymatous soma, which may attain huge dimensions, and a mass of considerable weight (*Macrocystis, Egregia, Phyllospora, Lessonia, Durvillaea*); even as a mass of 6 lbs. weight on British shores (*Saccorhiza, Laminaria Cloustoni*).

(2) With copious ramification (dichotomous or monopodial), erect arboreal trunks (*Lessonia*); fruticose or shrubby (*Cystoseira, Sargassum*); able to stand erect without the mechanical assistance of gas-bubbles (*Cystoseira ericoides, C. fibrosa*, &c.).

(3) With radial organization; apical growth, more or less 'dominated' by 3-sided apical cells; secondary increase in thickness; meristems and annual increment (Fucaceae, Laminariaceae).

(4) Specialization of ramuli as 'leaf-members' of high grade (as far as what has been termed the 'fifth degree').

(5) With rhizoidal attachment, or specialized exogenous or endogenous crampons presenting apical growth and dichotomous ramification (Fucaceae, Laminariaceae).

(6) Differentiation of 'trichome'-members, vestigial from more ancient filamentous phases (Mucilage-hairs, Sporangia).

(7) Inheritance of many cell-factors from more antecedent plankton-phases (including flagellated male gamete).

(8) An intracellular conduction-mechanism for soluble carbohydrates (downward current); perforated 'sieve'-tissue for proteid-conduction (Laminariaceae).

(9) Photosynthetic mechanism, including starch-storage in the chloroplasts (Characeae and Siphoneae); accessory colour-pigments of the chloroplast in variety.

(10) A capacity for reduction-derivation of pulvinate and disc-types of prostrate thallus; dorsiventral shoot-systems, 'rhizomes', and frondose phyllomorphic systems.

(11) Reproductive organs in an advanced condition of Heterogamy; flagellated zoïds specializing as sexual cells (*Fucus*); even gradual and entire loss of flagella (cf. *Dictyota*, Florideae); the oosphere as large as the female gamete of higher mammalia (*Himanthalia*, *Sargassum*).

(12) Fertilization *in situ* (*Chara*, *Florideae*).

(13) Post-sexual nutrition of a parasitic zygote (Florideae).

(14) Complete loss of somatic organization in the parasitic diploid phase (*Trophocyte* of Florideae).

(15) Differentiation of special reduced ramuli to bear the sexual organs (gametophores, antheridiophore, carpogonial branch), or the asexual units (sporophores, stichidia).

(16) Cytological sequence of haploid and diploid phases in two equivalent individuals (Homothallic alternation, *Dictyota*, Florideae).

(17) Dimorphism of the generations (Heterothallic alternation, *Cutleria*, Florideae); elaborated in three phases, and often involving four individuals (Florideae).

(18) In all cases of heterothallic differentiation, the individual derived directly from the zygote is the one which begins to diverge from the type, and expresses *deterioration*, induced by parasitic habit (Florideae), or as a phase of perennating organism (*Cutleria*).

(The list may be variously extended; the above is only intended as a sample summary, and is by no means exhaustive.) All these factors being the expression of the *normal equipment* of marine phytobenthon, they may be variously combined: the most highly specialized types are those which present them in greatest numbers; there is no reason why they should not all coexist in some culminating form. One would not be surprised to find any day a wholly new type with any combination of the above factors; and large numbers probably still await collection; but the probability of finding one with a *wholly new factor*, not yet recognized, tends to diminish. Hence the races of marine phytobenthon of the older seas may have attained to all these factors, and have divided them variously among their genera and families, but need not have been exactly like any algae we know at the present time, as the few surviving relics of 'green', 'brown', and 'red' series. For phyletic purposes the factors are the units, and not the individual forms.

Such a list again affords a general idea of what the sea has done for plant-life; and from this class of vegetation Land-Flora was evolved; there was in fact nothing else for it to come from. Marine algae are not few and feeble attempts at plant-construction, like those of fresh-water ponds; they are mighty races which have initiated and successfully evolved probably all that goes to the making of what we have learnt to call a 'plant'. The idea that all these factors, largely the commonplace of Land-Flora, should have been evolved in the sea, to run to waste, and that they require to be again invented under entirely different conditions in the evolution of larger

land-plants, from such depauperated relics as a fresh-water alga (*Coleochaete*), or retrograde Bryophyte (*Riccia*), shows so remarkable a lack of insight into the more fundamental principles on which life has been evolved, that the rise and persistence of such views may well remain a historical curiosity of the science.

Reasoning again from the analogy of the parallel and contemporary transmigration of animal phyla; the highest races of the sea survive to give the highest races of the land: it was the fish, as the highest and most efficient form of marine zoobenthon, which progressed to the amphibian of the land; marine Arthropoda become air-breathing as Insecta, and marine Mollusca may become air-breathing snails; but such types retain their more fundamental scheme of organization with little change; as man, in the wider sense, is but little removed from the fish. That is to say, it is to algae which express the culmination of all marine benthic factors that we have to look for the transmigrant parent forms of higher Archegoniates: Filamentous algae and inferior types may survive the transmigration, and remain as algae (and Fungi) of the land; but the race that went ahead was the best the sea had produced; or, it may be now said, *can* produce. It may be noted that the gradual emergence of the first land above the water represented a state of affairs that could never be repeated in the world's history; and may have involved a state of vegetative organism which similarly can never be exactly repeated. Land which has so arisen, to be colonized and so far occupied, does not again present the same opportunities to invasion, as 'made ground'; nor will there be the same necessity for meeting the initial problems. While residual races in the sea still compete with each other, and some races may fail, as others keep to the front; the paradox of the sea remains, that the comparatively older races, still dominant in the optimum stations on our shores (as isogamous Laminariaceae), were not the transmigrant forms, so much as types in which the strain of competition had already led to complexities in sexual reproduction and the life-cycle, as better represented in modern Florideae of reef-pools. In more Northern Latitudes our views are apt to be restricted by the fact that the dominant forms of vegetation of these seas, on which our first conceptions of marine life are necessarily founded, are again cold-water types of lower order; while the actual transmigration was undoubtedly effected in tropical water, under the stimulating action of intense insolation and the highest surface-temperature of modern seas (80° F.).

VI

THE MARK OF THE TRANSMIGRANT

THE progressive lifting of the sea-bottom, rising as a continental land-mass, densely populated with all forms of life, under optimum conditions of temperature and photosynthetic nutrition, over an indefinite period, expressed as many millions of years, or any such inconceivable space of time, is too vast a problem to be readily grasped, much less to be condensed into half-a-dozen pages; but the ordinary drying-off of a tide-range affords an analogy on a diminutive scale, at a rate that can be followed in a summer afternoon, and is a phenomenon of exactly the same nature, so often observed as to be relegated to a commonplace in this country.[1]

[1] The great elevation of the Himalayas, approximately 30,000 ft., is of com-

The change in the physical factors affects the whole life of the area uncovered, a sample of the surviving vegetation of the sea, in all its various phyla, from microscopic and bacterial plankton to the larger Laminarians, as well as innumerable animal forms: and it begins to be clear that all phyla which have attained the land-habit, including all the plankton-flora of fresh-water ponds, terrestrial diatoms, slime Cyanophyceae, fresh-water Chlorophyceae, Fungi, and all classes of Higher Plant-organism, have similarly derived their special characters from a passage through a condition of marine exposure ('Transmigration'); and although a certain amount of local 'migration' may have obtained, and may still follow any open route from the sea, as in the case of migratory fishes, such migration is of very minor phyletic importance, and cannot be postulated as the general case. The simple method of initiating not only a 'Land-Flora', but a system of 'Land-Vegetation', covering the entire range of the Vegetable Kingdom in immediate complexity, is the only problem worthy of consideration.

A doubt which seems to arise directly in the minds of most people who discuss this subject involves the question as to what becomes of the salt-content ($3\frac{1}{2}$ %) of the sea-water; and vague ideas of the immense deposits of salt from a dried-up arm of the sea at once oppress the imagination with views of intensified osmotic concentration. The question, however, does not arise in this form; the gradual withdrawal of the sea, as on an ordinary tide-mark exposure, leaves the substratum of rock practically denuded of salt. Salt-deposits only accumulate in the bed of a dried-up sea in a rainless district: the whole problem of subaerial transmigration is based on the necessity of a damp atmosphere, at first possibly, but not necessarily saturated, and gradually becoming less so to the general conditions of the present day. With the sea free to retreat, and copious atmospheric precipitation, the difficulty is really exactly the opposite,—How to maintain any salt-supply at all, for the necessities of the growing plant on a rocky foreshore. To do this the hypothesis of a low tide-wave with periodic return, or wetting within the range of the splash, may be postulated in the more preliminary stages of the transition. Another disturbing factor is the question of *soil*. 'Soil' at this time was non-existent, even 'mud' as containing abundant organic residues can scarcely be defined. The exposed sea-bottom would consist entirely of primary rock, clean swept, or with a slight deposit of sand, generally or localized in hollows;[1] all else

paratively recent growth (Miocene); a lift of one foot in 100 years would raise such a mass in three million years; a period of time almost negligible in more fundamental biological problems (Vredenburg, 1910, 'Geology of India', p. 106).

[1] The first land to emerge was, in all probability, largely exposed coral-reef, with coral-sand detritus of calcified plant and animal origin, with corresponding highly specialized calcified reef-pool algae. Definite calcified algae have been described from the Lower Carboniferous rocks, of quite massive texture (Garwood, 1912, on *Solenopora*; Geolog. Mag. 1914, p. 265, *Ortonella*); and there is no reason to disbelieve that rock-building calcified algae, as also associated corals, may have been in existence long before any sedimentary rocks were established. The first appearance of such primary rock and reef-formations above the sea-surface may be placed in the Huronian Epoch (Vredenburg, loc. cit., p. 16, on the Dharwar of India).

It is important to realize that with the ions of calcium carbonate at saturation point in sea-water (Murray and Hjort, 'Depths of the Ocean', 1912, p. 177), it follows that any disturbance of the ionic equilibrium which removes acid ions, or increases the concentration of the Hydroxyl ion, will result in a precipitation of $CaCO_3$. Thus $CaCO_3$ will be deposited:—

1. on removal of the CO_2 of the water in photosynthesis, (α) in the wall-membranes, (β) on the surface of the plant, (γ) in the adjacent medium;

being still to be made by the decay of plant-life. The original substratum, other than rock or sand, would consist entirely of the debris of the dying forms, no longer slowly sinking, or removed by animal agency, as in the medium of the open sea. The capacity of such material for retaining salts (by adsorption), as well as moisture, by occasional washings by the waves, may be estimated from the observation of the still existing benthic vegetation of the sea, wholly unchanged in these respects; and this gives the first initiation of an organic substratum, from which it would be possible to absorb the physically retained water and salts and so gradually perfect the mechanism of the 'root', and from which the living complex termed 'soil' has been also gradually evolved.

When this happened we do not know; but it may be noted that just as aqueous presentation of life of some sort became conceivable when aqueous vapour first condensed on the surface of the earth, and as plankton-life passed on into benthon with the lifting of the ocean-floor to within 100 fathoms of the surface, so the *possibility of land-flora* began with all subsequent lifting of the substratum above the level of the water.[1] The same would apply to zoological migration; and the population of the first land-areas was in all probability effected by a similar progressive elevation of comparatively level sea-bottom; a process in which the existing fauna and flora remained relatively passive. It is this, again, that affords the clue to the peculiarities of the algal-flora of fresh-water and pond-types, which have apparently no relation whatever to the higher land-flora, and seem equally cut off from the surviving races of the sea; these also have passed through the lifting process, withstanding a less or greater degree of exposure to subaerial conditions. It is obvious that the sieve of such natural selection was terribly efficacious;

2. by the decomposition of animal organism with liberation of ammonia (Murray and Irvine, 1889, Proc. Roy. Soc. Edin. xvii, p. 79).
3. by bacterial decomposition of nitrates, (Drew, 1913, Journ. M.B.A., p. 479).

Deposition of calcium carbonate becomes the commonplace of early benthic life, as it becomes the distinguishing feature of higher animal organism; the precipitate being subsequently 'utilized' biologically for purposes of exoskeleton or endoskeleton. In the case of algal benthon, it is not the primary deposition which is remarkable, as the similar fixation of the material, and its secondary utilization for protection against intense insolation of shallow reef-pools, or as a mechanical support on exposed reefs. Any phylum of algae may thus give rise to calcified and rock-building forms. The fact that such algae are at the present day restricted to the Florideae (*Lithothamnion*, &c.) must not be taken to imply that calcareous rocks are therefore indications of Florideae. With the calcification of the polysaccharide cell-walls, certain consequences inevitably follow, more especially as expressed in impoverished nutrition (as the cell-contents may be darkened by the increasing opacity of the deposit, at first transparent); and more particularly in the fact that intercalary extension is prohibited. The plants thus only increase at their apices, or free surface, by actual cell-divisions, which in the normal case of 10–15 μ. cell units, will not produce more than 4–5 mm. growth in the year; on the other hand, plankton-fed coral has been known to grow 6 ft. in one year (Sollas). Calcified algae are therefore the most starved, and the slowest growing of their race: they may survive under conditions of surf, where no other plants can maintain holdfast, or on reefs in shallower waters with intense insolation; but in more favourable stations, other algae will grow on and over them, still further increasing the starvation effect. The fact that such stony and incrusting algae are at present practically confined to the Florideae, only expresses the general starved habit of these algae, with high degree of specialization to counteract the wastage of their environment. That the calcified benthic animal-coral and the calcified benthic seaweed are contemporaneous, and always biologically associated, goes without saying; and the coral reef owes much of its $CaCO_3$ to plant-deposition.

[1] Cf. 'Huronian Epoch' (Dharwar of India), Vredenburg (1910), p. 16.

and as in the previous transition from the plankton-phase to that of the original marine benthon, the wastage of the struggle for existence was enormously increased. The more elaborately an organism is adapted to suit one set of environmental conditions, the greater the difficulty of re-organizing the equipment to meet an entirely different set of conditions; yet, in the long run, forms with the best equipment will survive. The increased wastage of the transition affords the next clue to the phenomena observed. The few races that survived only did so by pressing to the utmost any principles of economy in reproductive output that they may have previously initiated ('oogamy', 'fertilization *in situ*'). Problems of asexuality and post-sexual nutrition are again essentially the expression of response to wastage, and such become the commonplace of the life-histories of the more successful transmigrant races; so insistent that they are very generally accepted as the unavoidable equipment of a land-plant, though no such factors can have been evolved except as the result of life and death necessity. The maintenance of the reproductive output becomes the criterion of success, as indicated at first by a continued bare existence. All somatic organization remains stationary at the previous equipment, until the latter is secured; and no further progress can be made on older lines under the new conditions; that is to say, there can be no continued response once the complex of previous external stimuli is broken or removed; but when the possibility of existence under the strain is secured, new adaptations of an entirely different class may be effected among the survivors, as the expression of a new equipment for subaerial conditions, elaborated in response to the novel stimuli of the new needs of organism,—the special factors of Land-Flora as still higher types of plant-organism ('Xerophyton'). Reproductive efficiency requires to be maintained as it were over a latent period in the life of the race.

It should thus be evident, once the idea is grasped of the transition being infinitely difficult and rigorous, that the relatively few types which survived to populate the land, would be possibly so changed in the process that they may become very unlike the ancestral forms from which they were derived; and although some of the descendants of the latter may still exist practically unchanged in residual unaffected ocean, their kinship may appear wholly obscured:[1] while, on the other hand, features of secondary adaptation (as equipment of land-habit) may be so strongly impressed on the organism, that these may be mistaken for an indication of 'affinity', instead of simple biological convergence, as in the case outlined for the Archegonium or 'Seed-Habit'. The same, for example, applies with even greater force to the transmigrant heterotrophic races segregated as Fungi. The most cherished landmarks of botanical classification are at bottom possibly mere empirical and conventional expressions, which may afford but a poor guide to the facts of ultimate descent. For example, the distinction between *Equisetum* and *Lycopodium* may easily go back to distinct algal types of the sea, diverging long before the Archegoniate Era, as undoubtedly does that between Bryophyta and Pteridophyta, though equally 'Archegoniate'. Even the Angiosperms, so different in many respects from any Pteridophyta, may be again only linked to the archegoniate-series in similar distant marine-environment. The necessity for the broader view is everywhere apparent.[2]

[1] Cf. in somatic and reproductive organization the marine *Codium* and the transmigrant *Vaucheria*.

[2] Cf. Landsborough (1851), p. 81, pouring scorn on the atheistic and Lamarckian conception that the Land Oak (*Quercus*) should be derived from the Sea-Oak (*Halidrys*): yet *Halidrys*, as a *Cystoseira*, is in many respects as near the type of plant from which land-vegetation has been derived as can be readily found in British Seas.

The point remains:—How are the plants which have survived the ordeal as land-forms to be distinguished from those which have never left the sea at all? The test of the action of these subaerial selective processes may be suggested by the previous comparison of *Chara* with the Archegoniatae. The first indications are traced in the intensified economical specialization of the reproductive mechanism, followed by the elaboration of a perennating resting-spore, with protective cutinized exospore, capable of enduring a considerable range of desiccation and removal from the aqueous medium. That aqueous protoplasm should be able to concentrate, and to reduce its water-content from 90% to possibly less than 10%, seems almost incredible from the standpoint of the aqueous medium to which plasmic life is the original response; and the case of air-dry seeds is such a commonplace of subaerial life, that the land-botanist is often startled on realizing that there are no such 'resting-stages' in the sea. For example, in Phaeophyceae and Florideae, the dominant algal races of the modern sea, a 'resting'-spore is unknown; cuticle is unknown, and there is naturally no special adaptation to resist desiccation in a medium which never changes.

An interesting example among residual Chlorophyceae is afforded by the case of *Vaucheria* and *Codium*, commonly associated among the Siphoneae: yet *Vaucheria* is an advanced transmigrant, however much some forms may also endure on the mud of salt-water estuaries; the thallus is reduced to a mere plexus of coenocytic filaments, and reproduction involves oogamic fertilization *in situ*, with a thick exospore (3 μ) on the resting zygote, 75 μ diam. *Codium tomentosum*, on the other hand, is one of the finest of indigenous green sea-weeds, attaining a massive bush-growth up to 2–3 ft. in diameter, under favourable conditions, and reproduces by only slightly heterogamous flagellated zoïds; the zygote (20 μ) 'germinating' directly. The very use of the word 'germination' is at fault, in dealing with the types of the sea; the conception being purely subaerial, and a product of the transmigration, so commonplace that its secondary value escapes notice.

No such substance as 'cutin' occurs in the equipment of marine phytobenthon, any more than does 'lignin'; though many plants may show obvious indications of a laminated external membrane, which presents all the general appearances, and may be readily stripped in sheets from the subjacent tissue; in the dehiscence of gametangia (*Laminaria, Scytosiphon, Dictyota*), it may be even 'lifted' automatically, to the extent that the 'stripping of the cuticle' appears the obvious mode of describing the phenomenon. But the chemical alteration of the membrane which renders it impermeable or gas-proof, as in the typical cuticle of the land-plant, is wholly wanting.

The production of a cutinized resting-spore is the first rough test of the transmigrant, initiated as a perennation-phase, in chance of loss of casual water-supply, as the obvious adaptation to a life-and-death problem in the continuation of the race. The fact that such spores are generally characteristic of fresh-water algae, apparently obligate in a watery medium, has perhaps obscured their significance in the past, but does not affect the question. It merely implies that such forms live in water when they can get it. Fresh-water algae with resting-spores are not migrant from the sea, but are a constituent part of 'Land-Flora'. The true 'migrant' retains the original type of reproduction unchanged, and all its spores are adapted for immediate 'germination'. As previously noted, our conception of 'germination' is at fault, being originally gathered from the study of seeds (!); and even in its extended botanical significance, based on the consideration of land-plants, all similarly faced with the water-problem. The origin of such an investment is clearly to be traced in a further development of the 'Cyst'-stage, as the expression of the accumulated debris of metabolism in failing organism. The gametes, more and more differentiated as limiting

oospheres, are increasingly non-metabolic, and die off if not fertilized; and even on fertilization a similar period of diminished activity may supervene, as the response to progressive deterioration of the environment which had previously initiated the reproductive phase. The 'maturation' of the resting zygote thus represents a down-grade period, with accumulated debris to form the thickened wall, together with other katabolytes which endue the outer lamellae with its special resistent attributes, as the original lining wall may persist as an 'endospore'. The resting stage is thus always secondary, and normally follows sexual fusion as an inevitable consequence; though a similar resting stage may be attained in much the same way in any failing unit, as a 'Cyst,' or 'chlamydospore'.

That very similar conditions may obtain in the sea among flagellated phyla of the plankton is also obvious; such stages being distinguished as 'Cysts', or resting-spores, and are again usually expected to occur, even if they have not been otherwise described, in the case of flagellated forms of fresh-water (Senn [1]). An admirable example is afforded by the encystment of the fresh-water Peridine, *Ceratium hirundinella*,[2] also unique in presenting a resting zygote. The fact, again, that cysts are infrequent in the sea does not necessarily imply that such stages are wholly unknown, since encysted flagellates will similarly represent the enclosure of failing organism with a thick wall of katabolic polysaccharide debris, and all such forms will tend to sink to lower levels and so elude capture. The association of a cyst-stage (as auxospore) with other mechanism of sexual reproduction of failing organism is, again, very suggestively illustrated by the remarkable story of the Diatom *Corethron Valdiviae*,[3] described by Karsten (1904), as possibly flagellated and sexual in deep water, and sinking with the chance of dispersal by rising currents.

While exceptional cases of cyst-elaboration among pelagic plankton pave the way for the more definite utilization of the mechanism in the case of organism failing in transmigration environment, the rule still holds good, that marine algae (phytobenthon) do not present such stages; they are unknown in the great phyla of the Brown and Red Series, though in all such cases, the material for the initiation of such a phase is provided by the equipment of the sea; but it is only in the transmigrant that the latent capacity is called into operation, and rendered completely efficient in a new degree. Thus, in the case of the transmigrant Green Algae of fresh-water (*Oedogonium*, *Chara*, *Coleochaete*, *Vaucheria*, *Volvox*, *Hydrodictyon*), thick-walled spores become one of the most conspicuous features of the life-cycle, and the resting-spore is normally intercalated in the zygote; affording the accepted deduction that the resting-zygote closes the life-history of the individual, as also illustrating its seasonal periodicity.

In this respect it becomes possible at once to draw a sharp line of demarcation between the great biological classes of plant-life as:—

I. The **Thalassiophyta**, as the plants, predominantly 'Thallophyta', which have been evolved in the sea from the plankton-phase to that of marine benthon, and have retained their biological station unaffected; the latter as 'sea-weeds' with benthic equipment superposed on the equipment of the plankton-phase; and—

II. **Xerophyta**, as comprising land-vegetation in the broadest sense, all presenting a 'water-problem' in their economy, and not merely Bryophyta, Pteridophyta, and Phanerogamia, but comprising plants of all grades (inclusive of plankton and benthic forms of fresh-water) which have

[1] Senn (1900), 'Flagellatae', in Engler and Prantl.
[2] Pascher (1913), 'Süsswasser-Flora'.
[3] Karsten (1907), 'Valdivia' reports, ii. 2, pp. 110, 114; Berichte xxii (1904), p. 544.

survived the subaerial transmigration, to grow as best they can in media other than that of the sea; retaining in their respective cases the equipment of marine plankton, or the equipment of marine phytobenthon, *plus* that of their new acquisitions in response to subaerial conditions, as factors of somatic and reproductive organization wholly different from anything produced in the original environment of the sea; the most obvious and most readily checked feature being the 'resting-spore' with differentiated exospore and endospore.

It is obvious that botanical generalizations have been derived in the past almost exclusively from the consideration of Xerophyton; the case of the Thalassiophyte has not been appraised at its proper value, as the representative of a more primitive order altogether; or what is worse, it has been interpreted in terms of conceptions based on the investigation of plants of the land. Views of plankton and benthon have been founded largely on the flora of fresh-water ponds and fresh-water algae, presenting types of organism so far removed from their original condition, that it is often only in the most roundabout way that it is possible to deduce the extent to which their factors (somatic and reproductive) are in any sense 'primitive' (Desmids, *Spirogyra*). To obtain primitive factors it is necessary to go directly to the Thalassiophyte: this is the justification for the intensive study of Marine Algae and Marine Phyto-plankton, which will in the future establish sea-weeds, more particularly Phaeophyceae, as the great central group of the vegetable kingdom, as expressing the link between the flagellated races of higher plankton and the xerophytic vegetation of the land. Speculations on the origin of plant-life on the land, ignoring the solution of the primary problems of plant-existence, remain wholly 'in the air'.

The term *Thalassiophyte*, a particularly elegant one, was first used by Lamouroux for sea-weeds (1812); and as he says,—'parce que je ne connois aucune dénomination qui leur convienne mieux'. It may be perhaps cut down to *Thalassophyte*, and the meaning extended, as Lamouroux would have used it, if he had known, for the entire flora of the sea,—from 'Ultramicroscopica' or the first recognizable living forms to the finished alga; and the entire range of such organism may be classed as Thalassiophyta[1] in the widest sense.

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[1] The word was written 'Thalassophyte', probably in error, by De Candolle (1835), and is admirably adapted to replace the objectionable Thallophyte (Sachs, 1870), which is quite meaningless when applied to high-grade algae, the somatic organization of which is far superior to that of inferior land-flora, and is really a relic of the crude outlook of the Early German School, in ignorance of marine vegetation, and the emphasis attached to 'stem' and 'leaf' in Nature Philosophy and the Morphology of the Goethe period. The term 'thallus' is used by Schleiden (1846) for fungi, and by De Candolle (1835) only for lichens, as an unbranched lamina opposed to a 'frond'. The ideas of Sachs (1870) were again based on Fungi and Lichens. Kuetzing (1843) preferred to call the algal soma a 'phycome', while De Candolle classed Fungi, Lichens, and Algae as *Amphigames*. The unavoidable correlative to Thalassiophyta would be *Chersaiophyta*, to cover the biological kingdom of land-vegetation in a much wider sense than the 'Land-Flora' of Bower (1908); but since such an expression, as usually pronounced, is not particularly euphonious or distinctive, and has been employed by Warming ('Oecology', 1909, pp. 136, 289) for curious xerophytic formations on 'waste land' (Chersophytes), an alternative may be sought. *Aerophyta* might be suggested, but it is not the air, so much as the absorption of food-salts from the ground, which renders the land-plant a success, or not; and many such soil-plants (*geophyta*) still flourish only in the sea. The term *Xerophyte* was used by Schimper ('Pflanzengeographie', 1898, p. 4) as complementary to *Hygrophyte*, for land-vegetation in which the water-problem becomes more obviously acute; but the water-problem, as a matter of fact, as including contained

General Conclusions.

(1) The whole of the fundamental framework of the organization of a land-plant, the anatomy of its tissues, the morphological differentiation of members, as also the otherwise wholly inexplicable sequence of sexual and asexual phases in the life-cycle, are the expression of response to the conditions of marine environment.

(2) The plants which gave rise to Land-Flora were those which combined the factors of benthic equipment in the greatest abundance and perfection.

(3) No factor of somatic or reproductive organization evolved in submarine organism would be evolved in similar fashion, a second time, in the completely distinct environment of subaerial organism.

VII

WHAT PROBABLY HAPPENED

RETURNING to the analogy of the falling tide, undoubtedly the most remarkable and imposing botanical sight [1] this country has to show to a 'continentalist', it may be noted that apart from the question of maintaining reproductive output by increased efficiency, the more pressing problems are associated with:—

(1) The loss of the mechanical advantage of the medium for flotation and erection;

salts, is acute in all Land-Flora at some time, or has been the dominant factor in their evolution. 'Xerophytic' habit is but a question of degree, often again of time or season; a Hygrophyte presenting the seed-habit shows a feature which is the highest expression of xerophytic adaptation; and it is impossible to draw any sharp line between a xerophyte and a hygrophyte, much less by introducing the *mesophyte*, when all land-plants are xerophytic to a certain extent. In the limit it comes back to a question of the 'land-habit', and the extension of the term to include everything which has a water-problem in its life-cycle or phylogeny is only the ultimate phase of the subject. The term may be provisionally employed in this sense, in absence of a better, not as an expression borrowed from Schimper, or trespassing on his ground; but as an extension of the idea he had in his mind, in emphasizing the adaptations in subaerial vegetation to resist desiccation. On the other hand, it may be pointed out that the termination '-phyte' implies a *phyton*, or whole plant-individual, and may be conveniently retained for a phase of the life-history involving the organism as a whole. The special adaptation of details of anatomy and morphology, to which the term 'xerophytic' is more commonly applied, as a test of special response to environment, are more correctly included under the heading of *xeromorphy*, and the latter word has been employed in this sense (Warming, 1909, 'Oecology', p. 193). Since the subaerial transmigration includes the great central factor which underlies all subsequent expression of xeromorphy, as the greater includes the less, it may not be amiss to utilize this word, at once to indicate the primary evolution of Xerophyta, and at the same time to commemorate a pioneer biologist.

[1] Since at an extremely low tide, on a rocky foreshore, one is introduced to the sub-littoral zone, and can walk about in a tract in which plant-life is undoubtedly still very much as it was in the years before the geological record began, unmixed with any later intrusions.

(2) The loss of external water, and the immediate possibility of desiccation;

(3) The removal of the food-solution. All these factors press simultaneously on plants of all grades and of the most diverse lines of descent. Thus, it may be noted, that the mingled vegetation includes plankton-forms in vast variety, Cyanophyceae and Diatoms, filamentous Chlorophyceae, Phaeophyceae, and Florideae with more massive growths, disc-types, calcified types, shrubby forms and stout stems (as *Laminaria Cloustoni*) able to endure considerable desiccation; and among these, highly specialized shade-flora, largely Floridean, inured to circumstances of enfeebled nutrition, and hence already most economical with regard to wastage in the Life-History: it at once appears obvious that types with the elaborated factors of such 'shade-flora' (Florideae) will have the better chance of survival under conditions of malnutrition; while the massive Fucoids and Laminarians will in turn stand the better chance in virtue of their resistance to desiccation:[1] all others will vanish, or remain as relics in casual pools. The successful plant should combine the best factors of the Laminarian and Fucoid somatic organization, together with the economic life-history of the Floridean or Dictyotaceae; and, as a matter of fact, we know that roughly speaking this is what really happened.

The fact that elementary morphological relations were evolved solely in the phase of anchored marine benthon (hormon), and that such equipment once attained is not added to in the same way under conditions of subaerial environment, implies that as the plants of the lifted area were at the time, so they remained; and their successors, whatever they may have done since in other directions, will retain morphological indications of the biological horizon to which they had attained when the transmigration began. Thus:—

(1) Plankton-forms, left on dry land, live on as 'Plankton', or not at all: hence such terms as Cryoplankton, Dendroplankton, if far-fetched, may still be legitimate.

(2) Filamentous forms live on as filamentous forms, since the evolution of a massive soma was a submarine phenomenon: they do not change in this respect, except to retrograde in the manner of Desmids.[2]

(3) More massive parenchymatous forms retain the cellular organization to which they have attained as a basis for further adaptation.

Each type remains at its own benthic horizon; and the factors of the benthic habit are not re-created elsewhere; this follows from the conception of 'homoplasy'. Hence minute plankton-forms of all kinds maintain a precarious living in residual ponds, and chance accumulations of rain-water; ultimately perennating, when water failed, by 'resting-spores'; and in such manner fresh-water plankton (Volvocineae, Hydrodictyeae) have lived on, and specialized extremely beautiful types of suspended sphere-somata in quiet water, complex beyond anything of the sort possible in the more agitated surface-water of the sea; with, at the same time, an elaboration of oogamy, fertilization *in situ*, and complications in the Life-Cycle,

[1] Colloidal excess polysaccharides of the cellulose type, merely waste excreta and a nuisance in the early Plankton-phase, though attaining significance in the benthic habit as increasingly mechanically effective to anchored hormon, now prove the salvation of the emergent organism, the more efficient as the more hygroscopic, resistant, and rigid.

[2] Desmids may be accepted as the expression of secondary regression from a filamentous stage of conjugate Akontae. (Cf. West, 'Algae', 1916, p. 377.) A similar state of fragmentation has been observed in an Ectocarpoid migrant in a fresh-water tank as 'dismembered filaments'.

economizing wastage to the utmost limit of their possibilities. Plankton-Cyanophyceae, left as residual 'slimes', with little physiological or morphological specialization as benthic filament, remain as characteristic slime Algae (Myxophyceae) invested in elementary polysaccharide jelly, even on damp earth. Plankton-Diatoms may similarly survive on damp ground, to perennate in the absence of water with resting-spores as modified 'auxospores' (cyst-stages).

Filamentous algae, with little or no mechanical efficiency in their soma, may persist in pools formed by rain-water, as algal-types of ponds, streams, rivers, and fresh-water lakes, starved for food-salts, but with their photosynthetic character unaffected; or similar types may be relegated to the damp decaying mass of the substratum as saprophytic races of 'Fungi'. The latter stage will be even more readily attained by algae already existing under sufferance as endophytes and parasites in the interior of more massive hosts; and the same saprophytic and parasitic races subsequently bracketed together as 'Fungi', may be obviously of the most remotely allied algal series; e.g., as far apart to begin with as any modern Florideae and Phaeophyceae; as expressions again of the most widely differing types of filamentous organization, or less effectively massive and parenchymatous thallus. The possibility of such diverse polyphyletic origin alone suffices to show the extreme improbability of any hypothetical serial progression of Fungal forms, as visualized by a land-botanist, being ever in even the remotest sense the expression of any actual phylogeny or affinity. (De Bary, Brefeld.)

In all such lower forms of the sea the clue to the subaerial transmigration is to be sought in:—

(I) *Somatic decadence*, as the expression of:

- (*a*) Removal from the original food-solution.
- (*b*) Inability to withstand desiccation.
- (*c*) In the case of Fungi, an alternative mode of nutrition rendering all older somatic organization comparatively useless. With these may be associated:—

(II) *Special Reproductive factors*, as implying the limit of economic efficiency, whatever may have been the reproductive mechanism of the original algal-type, and expressed as further stages of an inevitable sequence, as:—

- (*a*) Extreme oogamy, leading to
- (*b*) Fertilization *in situ*, leading to
- (*c*) The Resting Zygote: or
- (*d*) Post-sexual nutrition, leading on to
- (*e*) A decadent parasitic (normally) diploid phase, leading to
- (*f*) The intercalation of the Resting-spore at the end of the diploid generation:

The final result being determined, in the first instance, by the level to which the reproductive efficiency and cytological alternation may have attained in the condition of marine benthon. Thus in the case of a form with a life-cycle of one phase (cf. *Fucus*), the Zygote becomes the resting-spore (*Chara*); in the case of a life-cycle advanced to two phases (*Dictyota*), the diploid phase will end with the resting-spore, following the adoption of fertilization *in situ*; this being the general case of higher Land-Flora, so long mystified as 'Alternation of Generations'. The example of the Florideae, with a life-cycle of three phases, suggests even the possibility of two stages with resting-spores, as closing the lives of asexual individuals, when that of the gametophyte is closed by post-sexual nutrition (cf. *Uredineae*). In all cases of difficulty it may be noted that—

(1) A cytological alternation of generations is a quite general factor of the equipment of the benthic phase.

(2) As the life-cycle was established in submarine environment, so it will remain unaffected through the subaerial transmigration.

(3) The new and most significant feature is the necessity for a *resting-spore*; and the fact that it must be intercalated most effectively in the reproductive mechanism, when the life-cycle is closed down to a single cell-unit, which may be set free for a dispersal-function.

Other extreme adaptations in the reproductive mechanism may be superimposed; cf. '*conjugation*' (Peridiniaceae, Conjugate Algae), '*siphonogamy*' (Fungi), '*spermatogamy*' (Fungi); and other resting-stages may be elaborated in the more vegetative soma (cf. sclerotia, gemmae, arthrospores (=cysts), chlamydospores); but by the above characters the types which have survived the subaerial transmigration should be readily isolated.

The special interest of the great subaerial transmigration naturally centres in the subsequent evolution of the Higher Land-Flora, as based on the possibility of increased powers of adaptability among the higher types of marine benthon. Previous examples make no real progress, their initial equipment being but small. With the removal of the water, and loss of its mechanical aid in erection and flotation, the first strain is felt in algae with less mechanical efficiency: those which are so strongly built as to stand up by themselves will not only be free from this difficulty, but in virtue of their massive texture will be the more adapted to resist desiccation (*Cystoseira*). In others a prostrate habit may become established: there is little chance now of acquiring an erection-mechanism in a marine plant which will not stand up; hence 'dorsiventral' forms may become general as following a line of least resistance, as also well-adapted to minimize desiccation. Turgidity is the only mechanical aid (*Nitella mucronata*), beyond massive deposits of polysaccharide, the more intensified as the insolation becomes more marked on exposure above the surface of the water; light remains the primary directive stimulus (*Chara*); the initiation of a subaerial 'balancing-mechanism' (geotropism) requires to be initiated gradually as the cytoplasm begins to feel its own weight; and automatic adjustment will naturally follow;—such automatic balancing being evidenced in a far older phase of plankton-organism, as expressed in Fibonacci symmetry (cf. Foraminifera). It is interesting to note that the original geotropic response will be 'negative', and in the main axis, and is not necessarily an inherent property of all cytoplasm. But apart from mechanical efficiency the effect of exposure will be most insistent in the food-supply: chance wetting remains the only source of food-salts, until an absorptive mechanism can be set up in the rhizoidal hapteron, and an upward current be induced by transpiration of the distal end of the shoot-system. Hence all rhizoidal types are doomed to inefficiency in this respect. No effective absorption can be ever attained, as expressed by absorptive (and adsorptive) area, nor a conduction-system be initiated, by a few cell-filaments of small calibre (10–20 μ diam.). Such types may persist in sub-saturated air; but no progress is possible along these lines to a higher horizon; and malnutrition, in spite of all optimum photosynthetic conditions, will be the predominant characteristic, and the clue to all the future developments of such races (Bryophyta).

It is to the more massive, more resistant, self-supporting perennial stocks of marine phytobenthon, with massive crampon-attachment, large and active photosynthetic area, that one must look for the greater possibility of somatic adaptation to the new necessities of the problem; and so far it will be among the higher Fucoids (*Sargassum*, *Turbinaria*) and

Laminarians that analogies may be sought for the factors making for success in the first land-types of true Land-Flora. The great thrusting power of the crampon-apex becomes valuable in a boring-organ, penetrating the débris of the substratum; and these structures express the precursors of the modern root-system; vestiges of the more ancient 'trichome'-system surviving as the 'root-hairs' familiar in soil-vegetation; though not necessary in the original case of a non-aerated mass of decaying substance, and so far rhizoidal in nature. The mechanism of secondary increase by a meristem ('cambium'), with continued seasonal growth ('annual rings'), affords the material for a conducting system (cf. slight suggestion of sliding-growth, and primary pits on tangential walls, of *Laminaria Cloustoni*), which only requires 'lignification' of its polysaccharide, and the new absorptive mechanism may be translated into a 'woody-cylinder.' The downward current restricted to extra-merismatic tissue ('inner-cortex'), gives the idea of 'phloem', with perforated 'sieve-plates' for proteid-conduction; and the essential features of a modern woody-stem are immediately foreshadowed, with no special suggestion or difficulty about the academic evolution of a 'stele'. Once an absorption-mechanism is initiated, there is no question of further decadence for want of food-salts; transpiration controlled by a 'cuticle' already existent, though not yet 'cutinized', gives the motive-power to the current, and adds to the concentration of food-salts, the more necessary as the food-solution becomes the more diluted by rain-water. Aeration of the more central tissues may be added at a later date, as the conducting system requires more oxygen; but the central tissues, previously starved for oxygen in the submerged condition, will at the least be no worse off than before. The initiation of intercellular spaces may be traced in the diminution of intercellular mucilages ('fucin'), as expressed in the dilatation of pneumatocyst-tissue (*Halidrys*, *Ascophyllum*) by the agency of excess photosynthetic oxygen. The essentials of a working-mechanism for elementary subaerial vegetation are readily outlined from such a fund of assets.

To such a somatic organization, given a segmenting apical cell (*Cystoseira*), leaf-members, shoot-systems, and gametophores (*Sargassum*), it is only necessary to add the ultimate biological economies of sexual reproduction, as oogamy, fertilization *in situ*, post-sexual nutrition, with a parasitic diploid phase, and the story of the Higher Land Plant is already outlined for the sexual individual. That of the asexual individual similarly presupposes the attainment of spore-tetrads (tetraspores) in 'sporophores', now becoming independent of aquatic environment, specializing further as the land-plant *par excellence*, developing internal archesporia (protected by an 'epidermis') in the sporangiophores, and so becoming the leafy plant with wind-distributed tetraspores. While the sexual plant in further stages, handicapped by the necessity of securing an external water-supply for the flagellated zoïd, under continued desiccation, tends from the first to remain in or near the water, and in a more saturated atmosphere may be expected to present phenomena of lignification and cutinization in a lesser degree, or by restriction to a wet-season period may never attain to such a level, as compared with the more subaerial diploid phase; or may be equally defective in full transpiration current,—the parasitic diploid phase, on its part, throws out its original basal crampons as it develops (just as the sporophyte of *Anthoceros* still throws out its vestigial rhizoids), and so escapes the doom of the complete parasitic decadence of the Bryophyta, to culminate as the arboreal vegetation of the land.

The weakest point of the story, at this stage, appears to lie in accounting not only for the 'non-progressive' character of the sexual individual, from

the first, so much as for its apparent steady deterioration. It is not that the gametophyte becomes decadent; there is no evidence in higher forms that it was ever specialized; and this has been always its essential characteristic; both 'lignification' and 'cutinization' of the subaerial sexual individual being wholly wanting. It is true that dimorphism of a 'heterothallic alternation' may be attained in marine benthon; but the known example of *Cutleria* presents a condition in which it is the *diploid* phase which becomes somatically decadent as a perennating 'disc'-thallus; and the phenomena can be never regarded as sufficiently comparable. But further considerations suggest that there may be a possibility of even a combination of 'reducing-factors', which come into operation in the case of the gametophyte, and not in that of the diploid (sporophyte) phase; for example:—

(1) The parasitic generation will more and more exhaust the parental soma, as it becomes the more efficiently parasitic. This is a factor already in operation in many Florideae, in which the apparent inferiority of cystocarpic plants has appealed to and puzzled many observers and collectors.

(2) As soon as the diploid phase establishes its crampons, it acquires a hold on the substratum, occupying the ground of the gametophyte; being on it, and so overshadowing it, and choking it out mechanically.

(3) These effects will be the more obvious as the gametophyte produces sexual organs at an earlier phase of somatic development; so that the gametophyte is restricted in growth, and will not endure beyond the first season, and hence may never become 'adult' in the sense of the sporophyte.

(4) Thus in the limit of reproductive economy, the gametophyte will be reduced to a young individual, presenting the minimum number of female organs to secure fertilization; and its development beyond this stage will cease the more quickly as the diploid phase initiates its independent growth; again the more prematurely as the gametophyte has less to supply it with. This is roughly the general condition of the Fern-prothallus at the present day; and the first exogenous crampon of the diploid embryo ('primary root') is differentiated as rapidly as the apex of the main shoot.

(5) The gametophyte stage thus tends in all ways, not so much to phases of deterioration and decadence as a condition of somatic inferiority, as to be relegated to a 'juvenile phase', as an individual precociously reproductive (cf. filamentous *Cutleria*, *Asperococcus filiformis*).

The reduction of the sexual organism to a 'juvenile phase' should again be interpreted in the light of economic production of fewer gametes; and *the fewer the gametes required the more extreme the apparent 'precocity' of the gametophyte*; the juvenile phase ultimately presenting the general effect of extreme decadence by the non-utilization rather than by the loss of somatic factors. In other words, it never grows up. Plants do not grow indefinitely large for the fun of the thing, but in order to reproduce their like at the wastage price. All successful organism works in terms of the 'Law of the Minimum', and as wastage is eliminated the soma is reduced. For all benthic organism, plant and animal, the recognition of the great 'Law of Benthic Waste' is the beginning of wisdom. The Fern Sporophyte is a large and bulky perennial organism, because the new phenomena of the wastage of its wind-dispersed spores is so enormous; the Fern Prothallus is relatively minute and apparently feeble, because it is so sexually efficient, having reduced its sexual wastage to a minimum. It is now interesting to compare the economic reproductive efficiency of a Fern Prothallus, which can secure a germinated embryo, attached to the substratum, in the same locus, and replacing the gametophyte, with an average expenditure of possibly half-a-dozen archegonia, and a few antheridia giving possibly not more than

a hundred antherozoids assuming the plankton-phase in a microscopic film of water, with the enormous sexual wastage and wholly indefinite chances of return of the million gametes of *Laminaria* and *Fucus*. Such reproductive efficiency in the gametophyte has been so far associated among Xerophyta with a practical suppression of the somatic organization of the sexual individual; the absolute limit and perfected ideal being, as a matter of fact, presented by the male prothallus of the Angiosperm, in which so far as this individual is alone concerned, there is *absolutely no wastage at all*; the organism being reduced to three nuclei only, all of which appear to be now indispensable, as all are used. When an individual is thoroughly efficient in a juvenile phase further growth is superfluous.

On the other hand, the asexual diploid phase assumes the progressive somatic organization of the land-plant, without the obligations of the sexual process; and in its turn becomes amenable to the inevitable sequence of economic progression. The story of the further stages of the evolution of heterospory as culminating in 'pollination *in situ*' and the inevitable 'seed-habit', being comprised within the history of the higher Archegoniatae.

The apparent weak point thus becomes on examination one of the strongest features of the story; since the necessity for, and the inevitability of, such deterioration appears fully warranted from several distinct standpoints; but above all as affording another view of the working out of the great benthic law of economy of wastage in its different expressions, as the clue to the progression of all 'higher' organism.

VIII

PLANKTON, BENTHON, XEROPHYTON

WITH what probably happened, however, one is less concerned, except to state the fact that, given the equipment-factors, every combination is possible; and in the chances of the struggle for existence of innumerable races and individuals, it may be always assumed that all the mathematical possibilities of the problem will have existed, given sufficient time for them to work out. In the case even of the origin of xerophytic land-flora from marine phytobenthon, time appears to be to our senses unlimited; that is to say, it is for all practical purposes far beyond the range of the geological record. With the vanished failures one has little concern, even as there may be no knowledge of them left. The case of the survivors is different; these, or rather their much-modified descendants, live and flourish, as the familiar land-vegetation dominating the present world. It remains to isolate the somatic and reproductive organization of these forms, and to determine to what combination of special factors their success may be attributed. It is impossible to prophesy from algae alone what is going to be the way out for the many problems involved; but the solution has been found, apparently more or less independently, by several distinct races of marine organism: the problems being met in so curiously analogous fashion, in quite distinct, though possibly not very distantly related phyla, that such higher plants have been commonly bracketed together as the 'Archegoniatae' and their derivatives; the mechanism of transmigration, as already pointed out, being often confused with the more essential original equipment of the benthic soma as an indication of affinity.

Summarizing much of what has been stated before:—

Three great epochs of world-construction follow as the result of the gradual cooling of the earth; the latter factor constituting the great driving-power behind natural selection; these are delimited by:—

(α) The aqueous condensation that formed the *sea*.

(β) The folding of the earth's crust that raised the sea-*bottom* (βένθος).

(γ) The ultimate emergence of *land*.

Plant-life, as also dependent animal-life, expresses a special response to these three epochs, marked by progressive advance as the conditions become more complicated, and a new phase is superimposed on the preceding, as:—

(α) *Plankton Epoch*, of organism in oceanic surface-water, involving one environmental factor only of *water*.

(β) *Phyto-Benthon*, the evolution of anchored (hormon) Sea-weed, implying the interaction of a second factor of *substratum*: and paralleled on the animal side by *hormon* organism and free-swimming derivatives as *nekton*.

(γ) The evolution of Land-Flora (*Xerophyton*), including in the widest sense all transmigrant vegetation, introduced to the new factor of *atmosphere*.

Each epoch shows its new and remarkable departures to meet the new conditions of the environment; each presents its special 'death-phase' as the result of failure. In each succeeding epoch, as specialization becomes inevitably more complex, so *wastage* is intensified. Elimination or reduction of the wastage-factor becomes the measure of 'higher' organization; but the highest forms, with wastage most efficiently economized in one epoch, are the more subject to the introduction of a new wastage-factor in the succeeding phase. These general relations of organism to changing environment constitute the fundamental framework of the 'life' on this world.

(α) **The Plankton Epoch** covers the evolution of a nucleated 'sexual' plankton or 'cell'-soma, from nothing at all but the ionized sea-water; there was nothing else to make it from; and beyond the cell, as a uninucleate protoplast, suspended as microscopic pelagic plankton in agitated water, life could not go. The epoch is thus narrowly defined, and plants in this state still fill the sea. The failure of such organism to maintain suspension involves sinking and death of the individual; and the death of all the individuals implies the death of the race.[1]

(β) **The Benthic Epoch** covers the evolution of the *thallus* or soma of marine algae, from the first encysted sessile flagellate to the organization of the multicellular body (*soma*) with members, tissues, and organs of special function, complex life-cycles, and reproductive mechanism specialized to minimize waste. The utilization of rising sea-bottom renders possible the sessile vegetating organism with secondary benthic equipment, which however returns to the flagellated plankton-phase for purposes of sexual reproduction and dispersal.[2] With the complication of an environment

[1] Self-preservation thus becomes the primary law of all living organism, as the simple result of one-factor (plankton) existence.

[2] Assumption of the benthic habit, at first undoubtedly the ideal condition from the standpoint of the metabolism of the individual, provided the substratum be well within the photic range, brings with it the unfortunate necessity for a *dispersal*-function. Organism arising from the free plankton of a moving sea cannot sit down and occupy the same restricted station for ever. Hence the return to the plankton-phase for processes of reproduction is quite as much the expression of the significance of dispersal, a necessity undreamt-of in the plankton-phase of stormy seas. As free-living animals ourselves, derived from nekton races of automobile fishes, we do not at first see the importance of this factor. Early animal races were equally benthic as

involving new consideration of substratum plus the effect of the original medium, a new type of organism arises in which a distinction may be drawn between somatic and reproductive tissues, tracts, or protoplasts; involving a further distinction between the mechanism of the individual and the organization of the race. Failure in reproductive efficiency introduces the new conception of racial extinction or decadence, apart from the survival of individuals, as suggesting a benthic death-phase.[1]

(γ) **The Epoch of Land-Flora** includes the vegetation of the emergent land, involving exposure to sub-saturated air, and introducing the water-problem (Xerophyton). While including in the wider sense all transmigrant organism, as plankton-forms of fresh-water, Algae and Fungi of the land; in the narrower sense it involves the story of the rise and progress of the Archegoniatae, culminating in the evolution of the Forest-tree (Gymnosperm or Angiosperm), as also the herbaceous 'Flowering Plant'. With the new factor-intensifying wastage in absence or loss of water-supply, a new 'death-phase' is added, as death of the tissues of the soma, in part, with the subsequent utilization of such units as skeletal and conducting mechanism. In the path of normal advance, such vegetation can only attain success by passing through the preceding phases; e. g. transmigrant plankton of the sea remains plankton on land; and only the highest types of marine phytobenthon, as forms possibly more highly organized in many respects than any at present existing in the sea, achieved the transmigration to meet the problems of the land and air.

The vegetation of the world at the present time comprises races which have passed through such a sequence more or less successfully, as the cut ends of a few surviving phyla. All present a narrow range about a certain horizon, and none is 'descended' from any other. Each follows its own line, and all lines may be visualized as running more or less parallel; but some have passed beyond the others. However suggestive 'phylogenetic trees' and schemes of 'linkage' may be in minor groups of closely similar organism, in the broader lines of phyletic connexion they are wholly fallacious. All indications of 'affinity' require careful analysis in order to ascertain the exact horizon at which they were acquired, as the inevitable consequence of certain conditions of growth and environment; since when acquired as such inevitable response to external stimuli they were necessarily polyphyletic; and many phyla at such an epoch may have presented phenomena of homoplasy. Speaking generally, it appears safer to regard a 'race' or 'phylum' as the expression of a group of organisms which derived their special attributes from the equipment of a preceding epoch, if not in one still further back. Thus all the main lines of what is now Land-Flora must have been differentiated in the Benthic Epoch of the sea (i. e. as algal lines), as all algal lines were differentiated in the Plankton-phase. The possibility is not invalidated that existing groups of Land-Flora may trace back their special line of progression to the flagellated life of the sea, wholly independently of one another (Pteridophyta).

Looked at from a slightly different angle, the higher types of land-

hormon Corals; attached Echinodermata, Hydroids, Polyzoa, &c., still abound, and the dispersal phase is normally provided for by the emission of ova and spermatozoa throughout the sea-phase of animal life.

[1] The Benthic-phase thus introduces the second and even greater law of biological life, as the *Benthic Law* under which the individual exists solely for the good of the race, and the race is forwarded at the individual expense. This, briefly, is why higher organisms live, whether plant or animal. The fact that any race still exists implies that the individuals collectively have done their bit.

organism, familiar to our senses as ourselves land-animals, were never evolved in any direct relation to the factors of subaerial environment; nor can they be regarded as conspicuously well-constituted for such a mode of existence: but they represent the only solution of the problem possible, considering the path by which they have attained their present position. The energy of growth, at bottom a phase of chemical (ionic) activity, supplies the driving-power of life, and such 'life' beats against the sieve of Natural Selection (De Vries); but this alone does not account for all the manifestations of plant-organization. *Twice* in the history of the world the sieve itself has been changed: the 'hidden hand' which did this, and so determined the path to be taken as a sequence of progression, was not 'Nature' or 'Divine Guidance', except in so far as such expressions may be utilized to cover an inevitable march of events, in this case merely the expression of the cooling of the earth, which (1) lifted the sea-bottom by tectonic changes, and (2) ultimately lifted the 'land' above the surface of the water, to be subjected to subaerial denudation to form 'soil'. While the plankton-phase includes the evolution of all cell-factors, in a manner which remains established for all future time; so in the benthic phase (sea-weeds) the entire theory of somatic organization (form and anatomy, members, tissues, and organs) is, in turn, so far established, that emergence on the land could only complete and finish off the lines of previous benthic specialization. Out of the many races evolved in the plankton-phase, a few only passed on to succeed in the benthic; of the benthic races still fewer satisfactorily made good and survived the subaerial transmigration. Thus, autotrophic phyto-plankton still includes many phyla of Green Flagellates, and over a dozen apparently fairly distinct races of 'Brown Flagellates'; but not one of the latter has any definite connexion with the Phaeophyceae, which alone passed on as Brown Algae; and no trace whatever is left of the Plankton-race that gave rise to Rhodophyceae. No Phaeophycean or Floridean passed on to higher autotrophic Land-Flora; and of the few algal forms that attempted to do so, no trace remains (except as *Chara* may show some suggestions). Thus, the known races are sharply cut off at both ends, and no known phyla of any specialization can be referred to any other; Diatoms, and Peridiniaceae as Protista, are as narrowly circumscribed as Florideae, without beginning or end. The modern discussion of phylogenetic evolution consists not in the enumeration of 'affinities' or 'resemblances', more or less suggestive to our perceptions, but in *the demonstration of the main path of physiological progression*, along which relics of possibly widely different phyla are scattered to point the way. Reduction of all wastage leading to the death of the race is the great problem to be solved for successful survival; with the initiation of the benthic phase (i.e., after the first wholesale change), the entire work of the individual organism is required to compensate the changes implied in such an alteration of the machinery of life. The old equipment has to be adjusted as it stands. Once removed from the environment to which it was the legitimate response, no further improvement can be expected along the older lines, and new equipment may be of an entirely different nature. The new equipment implies modified and adapted (somatic) organization; the method of counteracting racial wastage is included as 'reproductive organization'.

The only time that uniform Natural Selection had a clear field was in the Plankton-phase, the conditions being practically so uniform from the first commencement of 'life' in sea-water, that no abrupt change can be postulated; even as no breach of continuity can be postulated between the first 'living' organism and the physical organization of the sea-water; and the evolution of the cell was so far a continuous story. Failure in suspension, implying failure in auto-nutrition, is the determining factor in the evolution

of 'sexual fusions', holozoic nutrition, as also the evolution of the 'animal'. The life of the race responds to one set of conditions only (water), and the group of the Protista (mostly adopted by zoologists) covers the relics and further adaptations of the cell-individual in all future ages, whether pelagic holozoic plankton or largely transmigrant.

The Benthic-phase, following the first great environmental change, increases the complexity of two-factor life (*water* plus *substratum*), and the organization of the race has to be adjusted; the fact that the somatic (nutritive) part of the soma is elaborated independently of the reproductive mechanism, implies the introduction of a new condition of benthic waste and the inevitable consequences. The *Phyla* are determined by somatic (i. e. 'cell'), organization, inherited from the plankton-epoch; the condition of reproductive specialization expresses the level to which the race has attained in solving the wastage-problem: e. g., all Phaeophyceae have the same plankton-flagellate, but they differ widely in degree of reproductive specialization, and hence may be said to constitute a distinct phylum. The greatest fallacy of Classification in the nineteenth century has been to mistake a 'reproductive phase' for indication of 'affinity'. Broader lines of affinity are expressed more clearly in somatic equipment; phyla are grouped by the inherited features of their preceding history; once clear of the original plankton-environment, every somatic factor is derivative, adapted, or newly provided for the new environment. Newer reproductive phases are progressive, and follow an 'inevitable sequence', in all phyla the same. Thus :—

(1) *Isogamy*, the original reproduction of the plankton-cell, or the fusion of equal gamete-individual flagellates, passes on to the differentiation of gametes as Heterogamy.

(2) *Heterogamy* inevitably leads to oogamy. Oogamy, sooner or later, by failure of the mechanism of discharge, leads on to *Fertilization in situ*.

(3) The latter implies '*Germination*' *in situ*, and post-sexual nutrition of

(4) A parasitic generation. The parasitic generation is not repeated (a parasite on a parasite being an impossible situation for racial progress); and the second generation utilizes *asexual* discharged spores, in order to satisfy the need of dispersal. Since sexual plant on sexual plant would inevitably lead to failure, an 'alternation of generations' is equally inevitable in all lines of ultimate sexual differentiation. Different groups of modern algae have travelled different distances in this path of progression, according to their need of economizing wastage; e. g., the Laminariaceae, which still withstand primary benthic wastage in the full beat of the surf, retain the primitive isogamy, and are still dominant in cold rough water. Reef-pool forms of the tropical seas present the most advanced types of Life History (Dictyotaceae, Florideae), with relatively small and highly efficient mechanism. Sexual fertilization can go no further than oogamic fertilization *in situ*; and whenever this happens it is settled once for all. The Flagellated zoïd may be lost, even in the sea, being replaced by spermatogamy in Florideae; only highly specialized land-plants (Fungi and Angiosperms) pass on to siphonogamic mechanism. The highest animals, on the other hand, remain curiously benthic in this respect; Man is but a step from the benthic fish, and human reproductive cells (ovum and spermatozoon) are closely comparable in dimensions with those of *Himanthalia* and *Sargassum*.

On emergence to the land, environmental conditions are wholly changed *a second time*, giving life of three factors (water, substratum, and air). The mechanism of response is still more complex; a new wastage-factor (want of water, salts, and combined nitrogen) is introduced; the old equipment on hand requires to be adjusted, adapted, or replaced, on entirely novel lines. The multicellular soma is now so elaborate that it is maintained on much the

same lines, though it may become greatly complicated in further detail. Processes of conduction and absorption, involving roots and tracheides, are initiated; and such departures are superimposed on a sea-weed soma. Reproductive processes (sexual) can go no further, and remain stationary at flagellated fertilization *in situ* (though subsequently deteriorating in details of this mechanism). New departures relate to the air-problem (wind), as also want of water, including absence of food-salts with starvation-effects in the aquatic phase, and in turn repeat an 'inevitable sequence' of the struggle against wastage. The preceding asexual reproductive mechanism (isosporous in 'tetrads') is adapted for aerial dispersal. Tetraspores of the sea become 'Homosporous', air-dried, and wind-borne; and the mechanism of reproductive efficiency repeats itself in terms of the new and intensified wastage-problems of the air. *Homospory* inevitably leads on to Heterospory. *Heterospory* sooner or later equally inevitably leads on to germination *in situ*, and pollination *in situ*. The 'seed-habit' follows with its dispersal-phase, also as an inevitable consequence. All phyla must follow the same progression; no other is possible. Individual races of the present day may differ in the degree of attainment; but the highest have all come the same way, and the lower have been stopped at some intermediate phase, owing to some imperfection in their original equipment. The reproductive horizon is again no test of 'affinity'; the phyla are to be determined by the nature of the somatic organization they have inherited from the benthic phase (i. e., as sea-weeds); and flagellated zoïds of the preceding plankton-epoch, inherited more or less unchanged from the sea, may be traced in the male gametes as the last indication of the independent origin of whole phyla. (Cf. Bryophyta and *Chara*, isokont; the multiciliate sperm of Filicineae, and the isokont flagellate of the Lycopod and *Selaginella*).

The general scheme of plant-life can be thus plotted across three epochs, with progressive reproductive horizons, the phyla being of high grade, or backward, cut off behind or incapable of advance, each along its own path, irrespective of the progression of others, and tracing back to an independent origin in the sea, the full story of which is now beyond recall. In introducing these conceptions of the distinctive vegetation of these three world-periods of indefinite duration, the terms proposed may be said to worthily commemorate three of the greatest pioneer biologists of the present generation, who first drew attention to the essential significance of the problems concerned, although the latter may not have been formulated exactly in the manner to which they are now extended in a more precise botanical form,—as the 'Plankton' of Victor Hensen, the 'Benthos' of Ernst Haeckel, and the 'Xerophyte' of A. F. W. Schimper.

The following general principles may be accepted:—

(1) It is difficult to conceive of the same factors of organization being evoked as a response to two entirely different sets of environmental conditions.

(2) Every new equipment factor can be only attained as a matter of life-and-death necessity to the organism and the race of which it forms a part; i. e., in every postulated stage of advance a life-and-death necessity requires to be demonstrated.

(3) Every new factor is necessarily the adaptation by partial failure, or by improvement, of some previously existing complex mechanism.

(4) Hence no feature of somatic organization or of reproductive mechanism, observed in the case of higher organism, was ever designed from the beginning to meet the special circumstances in which it may be now functional.

(5) Teleological interpretations carry their own condemnation.

(6) Conversely, it may be fairly assumed that every factor of form and physiological mechanism had originally some function other than that it now performs[1] (cf. Chlorophyll, tracheides, stomata, phyllotaxis).

IX

THE STORY OF THE SURVIVORS—THALLOPHYTA

As previously indicated, in addition to the progression of higher races in the new environment of subaerial existence, multitudes of lower organism have apparently passed through the stages of the subaerial transmigration; and have succeeded in maintaining a more or less precarious existence in fresh-water, or under conditions of a saturated atmosphere, or even enduring considerable desiccation; living as best they can, with minor adaptations, though never getting much beyond the somatic equipment of the sea, and subject at all times to the loss of the external aqueous medium which contains their food-salt supply; to perennate in many ways, with so-called 'resting-stages', as the Thallophyta of the Land and Fresh-water; essentially of plankton and benthon-habit; it is true, but so far as they now acquire a '*water-problem*' in their life-history, to be included within the conception of the Xerophyton of the land. Such transmigrants of fresh-water, with wholly submerged existence, taking the risk of perennation by encysted zygotes and chlamydospores, comprise but deteriorated versions of algal organization, which have commonly passed for 'primitive' in virtue of their small size and apparently simple somatic differentiation. Where fresh-water supplies are practically permanent, and have been so for ages, as in larger rivers and lakes, elementary plankton-forms may persist practically unchanged, as also more elementary filamentous benthon, save for the starvation-effects of an enfeebled and greatly diluted food-solution: ordinary river-water presenting a salt-content very approximately one two-hundredth that of the sea.[2] Where pure rain-water is the only source of

[1] Analogies are not wanting in other provinces. The everlasting piling of adaptation on adaptation, which is the 'progression of life' under progressive change of environment, is paralleled by the fact that the material of sedimentary and even primary rocks may have been used up, denuded, and deposited, over and over again in the course of the history of the earth's crust (Geikie). In all ultimate stages of elaborated and modified organism, some little details of the general plan remain unaffected; as a great building may be constructed of any materials, or used for any secondary function; but certain factors in its original plan, as for example its orientation, will remain unaffected for all time. In the same way, the eye of a man is but the inheritance of the stigma of a vestigial photosynthetic chloroplast; his nose, inherited through the benthic fish, is but the pointed anterior end of the first flagellate presenting such polarity, as his mouth is but the elaboration of the oral depression formed in response to the work of the anterior tractor-flagellum. The more fundamental the features of mechanism, the farther they carry back in the history of the race.

[2] Data for German Lakes, and the Danube at Vienna (Steuer (1910), Planktonkunde, p. 22).

Drainage-water from fields in this country (Rothamsted) ranges from 0·02 to 0·05%

water-supply, salts may be of microscopic quantity, though the supply of combined nitrogen from the air may be little impaired; hence beyond the general reducing-effect of starvation in somatic and reproductive organization, the race may continue indefinitely at much the same level as that attained in the sea. Simple filamentous proto-benthon of the most elementary description is characteristic of Cyanophyceae, Conjugatae, and Confervoid Green Algae. In no case is there any suggestion of complex anatomy; even *Chara*, as a corticated filament, is simple by comparison with average sea-weeds; yet it appears so far ahead of other fresh-water forms that it is with difficulty included among Algae by land-botanists (West, 1916).[1] Extreme specialization of reproductive progression, with advanced oogamy and fertilization *in situ*, is also characteristic (*Volvox, Coleochaete, Oedogonium, Vaucheria, Spirogyra*), in otherwise most widely different alliances; and the zygote assumes the perennation-phase, with characteristic thick-walled 'exospore', so commonly as to pass for the 'normal' case; as marine algae with 'direct germinaton' are often regarded as anomalous by the subaerial botanist. But few cases of isogamy remain among the plankton-races (*Pandorina, Chlamydomonas*); asexuality, as also entire loss of the flagellated phase is characteristic of a wide range of minute Protococcoideae. Somatic deterioration and reproductive efficiency are the prevailing features; a few types emerge from the water in damp situations (*Vaucheria, Oedocladium, Chara*); but in no case do they become normal for such conditions, though much-enduring. Equally remarkable is the fact that no Brown Alga, nor any Red Alga, can be said to have passed the transmigration. The few Phaeophyceae and Florideae of fresh-water are merely inferior strays, as late migrants directly from the sea, presumably by the agency of aquatic birds (*Lithoderma fontanum*), or fishes (*Lemanea*). None of these types show the characteristic resting-stage, though undoubtedly enduring chance desiccation to a certain extent (*Batrachospermum*); as do also the marine algae of the tide-range. In all cases they are the most reduced and starved types of their series; no Phaeophycean is much more reduced than a *Lithoderma* disc-type in the manner of *Coleochaete*; no free-living Floridean is more minute in its organization than *Batrachospermum*; though extreme cases of epiphytic and endophytic *Chantransias* and *Streblonemas* of the sea may be smaller. All such types of filamentous benthon remain somatically at the level of their marine equipment; and the same applies to genera of plankton-organism. Diatoms of the transmigration remain Diatoms; as also Cyanophyceae persist as Cyanophyceae, so long as water is available; adaptations relate to different conditions of nutrition (salt-supply), and no advance to a higher phase is attempted. Of all Plankton-flagellates, or their derivatives, only two groups stand apart as presenting an advance beyond that of any marine type:—

(1) The multicellular Plankton-soma of *Volvox* (motile), and *Hydrodictyon* (immotile). The former a motile flagellated soma, presumably in part holozoic by flagellar nutrition; since with flagella acting in all directions equally, progression cannot be aimed at, and the spheres so far tend to be stationary. The latter a secondary, true, *plant*-soma, with recapitulatory flagellated expressions of great interest (Klebs); and both wholly unknown in the sea.

(2) The Desmid-type, as produced by the 'fragmentation' of filamentous

total solids, or 0·2 to 0·5 per thousand, as compared with sea-water at 35 per thousand, or $\frac{1}{175}$ to $\frac{1}{70}$ the salt-content. (Russell, 1915, 'Soil Conditions and Plant-growth', p. 66).

[1] *Chara* omitted from 'Algae' (West, 1916); 'British Fresh Water Algae' (1904).

benthon of the Conjugate order, with a secondary resumption of the plankton-habit (recalling the Diatom, though so widely different), and also unknown in the sea (West, 1916).[1]

To these may be added the interesting heterotrophic (saprophytic) series of the Mycetozoa, of amoeboid derivation, passing on to subaerial existence, and often attaining marked xerophytic adaptations by mass-aggregation, which have in the past caused them to be associated with plant-organism, as in the massive plasmodium of *Aethalium*; but retaining evidence in recapitulatory monokont flagellulae of the earlier phases of plasmodial aggregation found also in many low-grade Protista (amoeboid) of the sea and shore (cf. *Protomyxa*).[2]

Again, while reproductive progression in terms of advanced oogamy and fertilization *in situ* is well-established in the sea (Florideae), a new and special feature of reproductive mechanism, commonly passing as a decadent since non-flagellated phase, is characteristic of fresh-water, and is wholly wanting, so far as is known in the sea, as the conjugation of adults. Typically expressed in Conjugate Algae (hence legitimately termed 'Akontae'), it follows throughout the Desmid series, as also presenting the normal case for fresh-water Diatoms (the latter being with difficulty separated from neritic forms which may be remigrant as much as marine). The same process obtains in the only advanced Peridine of fresh-water (*Ceratium hirundinella*, a late migrant), and is still unknown in the sea; while it again characterizes quite independently the conjugate Fungus-series of the Mucorini. In all cases, apparently, the mechanism supersedes gamete-production as flagellated units; and, by a hastening of events, provides an enlarged zygote in the simplest manner possible, together with the advantages of a perennation-phase. In every case such 'conjugation' is freely accepted as clearly secondary, and an indication of extreme reproductive specialization, as *Spirogyra*, for example, may be said to have attained to a state of *siphonogamy*.

No type of plankton-organism, again, shows a wider range of distribution in pelagic and transmigrant environment than the Diatom, itself the most highly specialized autotrophic plant-cell of the plankton-phase. Yet no Diatom of fresh-water offers greater somatic specialization than that of types still dominant in the sea (neritic and pelagic). No land-Diatom approaches in organization the benthic *Schizonema*-forms, or the wonderful branching thallus of *Licmophora*. Similarly, fresh-water Peridines are of the most generalized description; *Ceratium hirundinella*, as a cosmopolitan late migrant and casual, is one of the few representatives of the more complex and holozoic Peridine-mechanism. It is to the marine types that one has still to look for the expression of the potentialities and range of the race. Fresh-water Diatoms are but the merest vestiges of the forms of the sea; the pelagic *Corethron Valdiviae* affords the best suggestion yet advanced for the archaic flagellated condition, produced as recapitulatory gametes, fusing in deep water (100 fathoms), apparently in the case of failing organism (Karsten, 1904),[3] and taking the chance of upward drift.

General types of algal plankton and benthon thus remain little affected, so long as a source of water is secured; the only effect is that of starvation-reduction, somatic deterioration, increased reproductive economy pressed to the limit of oogamy, and fertilization *in situ*. The resting-spore is normally intercalated as the zygote, following sexual fusion and failing

[1] West, Algae (1916), p. 377, 'dismembered filaments'.
[2] Proteomyxa and *Protomyxa*, Lankester (1909), 'Treatise on Zoology', p. 11.
[3] 'Valdivia' Reports, II. 2, p. 100; Berichte (1904), p. 544.

metabolism, as generally associated with the deprivation of water and salt-supply. Otherwise an enormous number of lower types persist in which sexuality is entirely abrogated, and the race maintains existence without sexual stimulus, and progresses at a rate of variation which may appear negligible; though it may be no worse than that of the progression of racial improvement before sexual fusions became general; the essential significance of sexual reproductions being probably traced in its action as a hastener of phyletic change, rather than as the sole causal factor.

While no transmigrant lower algae make any advance in subaerial growth, but merely endure the evils of the passage to the inferior stations of fresh-water and saturated air, one new and striking departure does obtain, in the assumption for the first time[1] of the so-called *saprophytic* habit, giving rise eventually to an entirely new race of organism, almost on a par with the first animal phyla, as the great biological series of the Fungi. A few Diatoms and Flagellate 'heteromorphs' are commonly described as colourless and therefore 'saprophytic' (West, Pascher, Provazek),[2] though on very slender evidence; the term 'saprophytic' being very vaguely employed: a colourless Diatom, for example, may be, as in the case of the 'variegated' leaf, the expression of reduction of the amount of chlorophyll only beyond the range of our colour-perception, or may represent the effect of the photosynthetic pigments being destroyed as fast as they can be renewed, without necessarily implying that all autotrophy is necessarily eliminated. The same applies to many minute forms in which colour-effects, as in the case of red blood-corpuscles, may be effective only when seen in mass-aggregations. But the case of the main Fungus-series implies more than a mere loss of chlorophyll in forms closely resembling known autotrophic types, and hence conveniently known as '*heteromorphs*'. The great majority of plants included under the expression 'Fungi' are obviously derivative from phytobenthon, sharing the essentially septate filamentous organization of the protobenthon of the sea, in which the protoplasts are invested by firm polysaccharide membranes, with even suggestions of chitinous material (as nitrogenous débris). The extent to which highly elaborated organic food-material may be absorbed through these colloidal polysaccharide membranes remains doubtful; it is sufficiently evident that such protoplasts cannot take in either colloidal proteid or starch directly through a colloidal membrane; though the effect of the action of enzymes, whether definitely excreted, or extrinsic (e.g. of bacterial origin in the medium), remains a possibility. Ordinary nutritive absorption is thus restricted to simple monosaccharide sugar and amino-acids, &c.; and the expression 'saprophytic' may be conveniently restricted to such metabolic processes, as delimiting it from the case of holozoic ingestion by naked plasma, or by flagellar action, more distinctive of elementary animal phyla. That all such methods of nutrition grade into one another may be freely accepted; just as the saprophytic fungus soon becomes obligate and holo-parasitic, taking fluid material directly from living plasma.

The critical factor determining the evolution of successful Fungi of the Transmigration is, again, the lack of water: emergence of the land, visualized

[1] The case of Bacteria omitted, as more obscure regressive saprophytic forms form protobenthon of the horizon of Cyanophyceae, exhibiting a plankton-phase of 'dismembered filaments' and cocci.

[2] West, 'Algae' (1916), p. 97; Pascher (1913), 'Süsswasser-Flora Deutschlands', Flagellatae, i, ii; cf. p. 93, *Lagynion* and *Heterolagynion*; i.e. since heterotrophic; also A.P.K. (1912) xxv, p. 198; Provazek (1900), Oest. Bot. Zeitsch., '*Synedra hyalina*'; Karsten, Flora (1901), p. 404.

as the withdrawal of the sea, implies for the first time that dead organisms are not immediately devoured by the multitudinous scavenger-life of the medium, and are no longer subject to the macerating effect of deep water. Dead algae do not lie about in the sea; even the condition of 'loose-lying' drift is only a minor problem of the colder seas; such material being so far alive or in 'cold-storage.' One of the first striking phenomena of the subaerial transmigration was the accumulation, for the first time, of masses of dead and decaying somata. Plants which died *in situ*, and were neither washed away nor eaten, not only accumulated to constitute the first 'soil' for the crampons of the survivors to bury themselves in, and spread out as 'roots'; but the decaying material becomes also a reservoir of combined nitrogen, of essential significance once the water had withdrawn, and rhizoidal filaments stimulated to nitrogen-absorption begin to take on a new function. In such a substratum of decaying vegetation, forms of lower algae, prostrate beneath the stronger axes, and shaded by larger photosynthetic laminae, find abundant organic food-material ready at hand, both carbohydrate and nitrogenous, to enable them to maintain at any rate an enfeebled existence. The somatic organization deteriorates to mere 'descending hyphae' (henceforward termed *mycelium*), so familiar in the basal regions of more filamentous Phaeophyceae, or residual from the axes of larger forms (cf. *Fucus*, *Desmarestia*) by the suppression of the photosynthetic cortical and superficial units, and little further somatic specialization is required. Morphological organization devoted to the production of cylindrical axes withstanding wave-traction, and bilateral laminae or systems of finely subdivided ramuli, devoted to the provision of increased surface exposure to the external salt-solution and incident light, also deteriorate to a vanishing point, though vestigial traces may long persist. Mycelial hyphae, absorbing directly from the decaying material, supply all the needs of the organism, and the Fungus-soma is so far foreshadowed, as presenting a somatic organization reduced to the simplest expression; only to become specialized in turn along new lines, under pressure of xerophytic stress, as the organism acquires adaptation by mass-aggregation, or by more densely 'sclerosed' polysaccharide-deposits, to resist the desiccation of drier air. Such a vegetative soma may be attained in any race of marine phytobenthon, from the highest to the lowest; and such origin is of necessity polyphyletic beyond any possibility of recall. Suggestions of algal (marine) organization can be only expected to be traced in reproductive phases, themselves equally liable to the effect of problems of intensified wastage. All stages of somatic aggregation of such filamentous habit may be expected, varying according to conditions of the transmigrant environment.

Nematophyton (Penhallow),[1] miscalled *Nematophycus* (Carruthers), of the Devonian and Carboniferous, is described as forming massive shafts 20 ft. high, and 2–3 ft. diam., the axes consisting solely of coenocytic tubules running vertically, 30 μ diam., mingled with mycelial wefts of segments 5 μ diam.; apparently a water-storing system with annual increments up to 150 years (Dawson).

Massive Polypori (*Fomes*) in this country may give perennating masses 2–3 ft. in diameter in old hollow tree-trunks; with no special adaptation except a texture so 'woody', that one almost expects to trace lignification.

Cf. Barber (1892), Annals Bot. p. 329; Dawson (1888), p. 42.

Under such novel conditions, far more extreme than the case of the starved transmigrants of fresh-water, the older reproductive methods of the sea will tend to be much modified, to appear as 'deteriorated' versions.

[1] Seward (1898), 'Fossil Plants', i, p. 192. Without a trace of photosynthetic surface-tissues, and nothing in the world like any Laminarian (!).

Sexuality may be abrogated entirely, as in smaller algae, or phases of extreme specialization may be attained; as fertilization *in situ*, spermatogamy, already familiar in Florideae, without implying necessary 'affinity' with such types, any more than 'conjugation' processes of larger immobile gametes (Mucorini) express any necessary relationship with conjugate (siphonogamous) Akontae; the ultimate phases of reduction-specialization and deterioration again tending to run parallel in all inferior biological stations; just as similar problems of subaerial environment may be solved fairly similarly in distinct lines of descent (*Homoplasy*). The new equipment of the race will thus be associated with (1) the difficulties of *heterotrophic nutrition*; (2) the problem of dispersal by methods of *subaerial distribution*; and (3) the possible loss at any time of the casual supply of fresh-water, at any stage of the life-history, as expressed in stages of *perennation*.

In dealing with such possibilities, few points are more impressed on the botanical writings of the last generation than the suggestion that the Ascomycetes are representative of marine Florideae; the idea being apparently initiated by Sachs (1874), and based solely on misconception of the suggested resemblance of fertilization in terms of spermatogamy (Eng. Trans., 1882, p. 305, 'Carposporeae'). Much as one may be anxious to demonstrate the derivation of Land Fungi from algal forms still existing in the sea, the greatest care is required not to over-state the case, or jump to absurd conclusions. 'Affinity' by 'resemblance' is the bane of the evolutionary systematist, as expressed in the construction of wholly imaginary phylogenetic types 'linking' living types in lines of descent. The case is the more glaring when it is based on crude text-figures, rather than on the actual details of the plant, or on the conventional phraseology of such a term as 'trichogyne', applied to several distinct types of conjugating organ. There is, for example, no evidence whatever among Ascomycetes or Laboulbeniaceae of the delicate 'mucilage-hair' process of the oogonial trichogyne of the Florideae, however much it may look like it when drawn on paper. (Thaxter, 1896, Monograph of Laboulbeniaceae, p. 220.) Nor is it reasonably conceivable that the sporangium of the diploid sporophyte phase, so universally restricted to the minimum of a single tetrad among marine Florideae, should be identical with, or the parent form of, the organ equally universally expressed among Ascomycetes as including eight ascospores following one act of meiosis. It may be also pointed out that no Fungus 'spermatium' expresses the case of the Floridean 'sperm', 'slipped in endochiton' from the parent organ; though the possibility is not invalidated that the latter may be abstricted whole in some of the most advanced types of the sea (cf. *Polysiphonia*, Yamanouchi (1906), Bot. Gaz. xlii, p. 411).

Widely accepted analogies between such types merely express ignorance of the marine forms, and the meaning of their detailed organization. *Haploid and diploid cycles, fertilization in situ, specialization of flagellated zoïds, reduced sporophytic phases and meiotic sporangia, are factors of the equipment of marine algae; they may be retained in land-transmigrants as vestigial, derivative, modified, deteriorated, or adapted to suit a new environment; retention of such physiological factors affords no strict guide to affinity, but merely expresses parallelism in progression along a well-defined course.* Fungi have been persistently looked at by land-botanists from the standpoint of higher Land-Plants, and have so remained a puzzle; even the nomenclature is borrowed from Land-Flora, with which they have no direct relation at all, save *via* the older sea-weeds; hence they should be only considered from the standpoint of marine algae, and the terminology of the latter may be legitimately employed.

While neither Ascomycete nor Basidiomycete, as the two great dominant series of modern subaerial Fungi, show the slightest direct affinity with any existing marine Algae; however much it may be certain that they were originally derived from forms actually existing in the sea, and retain an organization based on the factors of marine phytobenthon; it is interesting

to examine first the few Fungus phyla in which a flagellated zoïd-phase is still retained, as expressing so far the more primitive types of the series. The fact that no aquatic fungus with any claim to be regarded as primitive, beyond a few cell-parasites (as Chytridiaceae) of microscopic dimensions, persists in sea-water, sufficiently indicates that all aquatic Fungi are transmigrant to a certain extent; and are so far highly modified, as tending to express phases of oogamy, fertilization *in situ*, asexuality, and the introduction of perennating stages. It may be also pointed out that there is no evidence of any of the main phyla of modern *Fungus*-forms arising directly from known starved fresh-water algae; the origin of the entire series goes back to the period of the transmigration.

Of these types the **Monoblepharideae** are so far unique as presenting two cases in which fertilization *in situ* is still effected by a motile antherozoid; and in *Monoblepharis*, for example, the zoïd is described as monokont, with a single flagellum about two body-lengths; apparently vestigial, and exhibiting a 'hopping' movement, as if the flagellum acted as a propeller. Cornu's figure suggests that euglenoid activity is also effective. The oogonium is far advanced, with spherical oosphere, about 15 μ diam.; and the zygote assumes the encysted perennation-phase. Otherwise the type is closely parallel with *Saprolegnia*; and it is now difficult to follow any reasoning which might have seen in such a type any indication of 'affinity' with *Oedogonium* (Von Tavel, 1892).

In all other types, with the adoption of some form of conjugation or siphonogamic approximation, the zygote, being thus fertilized *in situ*, may follow on in the encysted perennation-phase, but no provision is left for the dispersal function; and a flagellated zoïd is commonly retained for this purpose, so long as the aqueous medium for it to swim in may be available as casual water-supply.

Thus in parasitic **Chytridiaceae** a zoïd closely resembling that of *Monoblepharis*, and apparently similarly deteriorated, since with similar characteristic hopping movement, is retained for the asexual phase; and such zoïds are liberated in considerable numbers from a unilocular sporangium. These zoïds, more or less rounded, range from 5–10 μ diam., but may be less (2 μ, *Catenaria*), while the single flagellum ranges 2–3 body-lengths (*Polyphagus*). Sexual reproduction (*Polyphagus*, *Zygochytrium*) has passed on to a condition of conjugation, and the zygote assumes the encysted perennation phase.

Similar conditions prevail among the still wholly aquatic **Saprolegnieae**; the sexual organs present an advanced condition of heterogamy, the oospheres in an oogonium ranging to as many as 40 (*Aplanes Braunii*), 20 (*Saprolegnia dioica*), or reduced to one only. Fertilization follows by siphonogamic conjugation, giving the encysted perennation-stage of the zygote. The flagellated zoïds are developed within a unilocular sporangium, in which meiosis may be expected to occur, and the zoïds are discharged as isokont units, with flagella again of 2–3 body-lengths; they are described as also motile in a stage with two laterally inserted flagella, suggestive of a further differentiation, though not fully anisokont, and they 'germinate' directly without a resting-stage. That is to say, the flagellated plankton-zoïd is retained for rapid propagation and *dispersal*. Observations are scanty on the details of the nature and origin of the flagella (cf. *Achlya*).

Pythium presents an interesting case, connecting definitely autogamous, aquatic Saprolegnieae with subaerial Peronosporeae, as a more distinct parasitic type of Fungus, with increasing tendency to a more subaerial mode of existence in a saturated atmosphere. The oogonium, at the limit of oogamy, gives an oosphere 15–18 μ diam., fertilized *in situ* by a siphonogamic 'antheridial ramulus'; and asexual zoïds are retained in an aquatic phase, which are curiously parallel with those of the Phaeophyceae; being apparently similarly anisokont, with anterior and posteriorly directed flagella of 2–3 body-lengths; while the unilocular sporangium may be detached bodily, and utilized as a 'conidium'.

The parallelism of such reproductive phases, with the general laws of progression in reproductive specialization in the case of marine algae, is sufficiently

obvious. The limiting terms of advanced specialization being associated with reduction and deterioration in the mechanism to a characteristic Fungoid and Phycomycetan method of shaping the Life-Cycle; the latter remaining curiously unintelligible, until it is viewed in proper perspective, as the modified version of an algal type, of the horizon of the simpler heterogamous Phaeophyceae or Siphoneae: these forms presenting merely the ultimate phases of deterioration of the saprophytic algal soma, with no new departures beyond the resting-stage of the transmigrant in casual water-supply.

Among the **Peronosporeae**, as presenting more advanced phases of parasitic and subaerial organization, following the same general lines of coenocytic mycelial habit, the same limiting expressions of oogamy, siphonogamic fertilization, and the perennating thick-walled zygote, the plants differ in that they are now adapted as plant-parasites living in less saturated air. The unilocular sporangia are greatly exaggerated in numbers; they are normally utilized directly as abstricted 'conidia'; and are successfully air-borne, as the first definite expression of a new mode of dispersal by the agency of the wind, rather than by movements of the water. So-called 'germination' of the 'conidium' in water may restore the flagellated phase, still apparently quite normal and anisokont. The large resting zygote (30–50 μ diam.) 'germinates' in a similar fashion; returning to the flagellated zoïd-phase again, or 'becoming a sporangium directly' if water may be available. But it is evident that the 'conidium' is the normal homologue of the asexual sporangium of *Saprolegnia*. New departures, so far, are connected with the perennation of the zygote in dry air, dispersal of the 'conidia' in moist air, and the germination of both reproductive stages in a watery medium to give the recapitulatory flagellate, as a convincing illustration of the tenacity of the flagellated stage in the Life-Cycle; though in absence of casual water-supply either, again, may 'germinate' to give the mycelium directly. The germination of large oospores by a 'tube', emitted from a pore, to give a coenocytic hypha, is but the identical state of somatic deterioration to be traced in the last phase of a germinating microspore to give the pollen-tube of an Angiosperm, and should be so regarded; there is nothing 'primitive' about such a construction; the mechanism in both cases being reduced to a minimum, as a parallelism in heterotrophic nutrition. On the other hand, the enormous development and apparent preponderance of the sporangial conidia is to be regarded as the expression of the attempt to cope with the increased wastage of the subaerial condition of dispersal.

Once such Fungi are regarded in their true perspective as the decadent survivors of marine algae, recapitulating the phases of reproduction initiated in the sea, and not as primitive plants, *sui generis* (the conception one obtains from De Bary and Brefeld), their special factors fall into line with the general problems of the transmigration, and acquire a greatly enhanced interest and value; affording in turn a remarkable insight into the history of those forms in which more complete adaptation to subaerial environment is associated with complete elimination of all flagellated phases, and with the more marked utilization of the mechanism of air-flotation as giving rise to what is more generally conceived as a 'spore'. The subsequent specialization of the reproductive mechanism in connexion with air-borne spores marks, in fact, the great key to all further progression in the group; and, as corresponding adaptations to economize the new wastage of the race, affords the clue to the higher grading of the sub-groups and existing phyla. That such flagellate-retaining phyla of Fungi are derived from marine algae of the transmigration may be regarded as sufficiently obvious, and, in fact, freely accepted; but there is no evidence whatever that they are to be directly connected (or 'linked') with any known autotrophic algae. Their features may run parallel in somatic deterioration, as in extreme reproductive specialization and economizing of the wastage-coefficient, but such parallelism in one or more factors does not constitute 'affinity'; and any association of

such filamentous Fungi with anisokont Phaeophyceae, or isokont Siphoneae, for example, is beyond the limit of even pure speculation. The general progression of benthic life of the sea may be still indicated, though overlaid with many new departures associated with:—

(1) the possible removal from water, giving encysted perennation-phases;

(2) the saprophytic habit, with loss of chloroplasts and 'cell'-organization;

(3) increased possibility of wastage in subaerial dispersal.

It is in these respects that the **Mucorini** acquire a special value, as representing the turning-point in the relations of the Modern Fungi to the new environment of the land. In that (1) they still present the complete and coenocytic deterioration of the simpler Phycomycete, with little new and special departures in the mycelium-stage; (2) the flagellated phases are henceforward wholly eliminated; while (3) they present a remarkable series of parallel adaptations in the solution of the three essential subaerial problems of *fertilization*, *perennation*, and *dispersal*: e. g.

(α) The fertilization *in situ* of a large gamete by siphonogamic conjugation of practically closely identical gamete-branches, much as in transmigrant and conjugate algae (Akontae), though wholly different in details of the mechanism.

(β) The zygote, which may be relatively enormous (*Mucor Mucedo*, 100–200 μ diam.; *Rhizopus nigricans*, 150 μ; *Sporodinia grandis*, 300–325 μ; *Phycomyces nitens*, 500 μ), is the perennating encysted stage, with highly specialized 'epispore' showing protective coloration, or outer investments of xerophytic nature.

(γ) Adaptations for subaerial dispersal are found in the unilocular sporangium, the contents of which, when few, may be ultimately associated with abstriction of so-called 'conidia' (cf. *Thamnidium*, *Piptocephalis*).

As a distinct class of 'conjugate' Fungi, the Mucorini are also remarkable as presenting two new departures of distinct significance, as correlated with the difficulties of special environment:—

(α) The segmentation of the mycelium into small free units ('Mucor-yeast') as a so-called oidium-stage, comparable with that of *Saccharomyces*, expresses a definite attempt at regression to the plankton-phase of immotile cell-units, as seen more particularly in fresh-water Akontae (Desmidiaceae), though also noted in a special case of migrant Brown Alga (*Ectocarpus*) in fresh-water, as a condition which may be paralleled in other groups; this 'sprouting' stage bearing no relation to 'fission', but representing the early abstriction of definite ramuli of a branch-system implying the antecedent attainment of freely-branched filamentous phytobenthon.

(β) While the development of the reduced unilocular sporangium as a conidium, in some forms may be compared with the air-borne conidia of the Peronosporeae, a new departure obtains, devoted to the same end, as the production of air-borne units for dispersal, in the actual primordia of what were originally flagellated zoïds; and definite immotile *endospores* are elaborated within the unilocular sporangium as units fulfilling the conventional conception of a 'spore'; familiar enough among higher land-flora, but again only so because it represents a parallel solution of the same problem of subaerial dispersal in a wholly distinct transmigrant series. The special features of the *Mucor*-story, being that such spore-units may be formed in enormous numbers, as about 1000 in the 300 μ sporangium of *Mucor Mucedo* (cf. the suggestive case of the unilocular sporangium of *Spermatochnus*[1] among the Phaeophyceae), as a phase far behind the condition of the limiting tetrad-spores of Land-Flora.[2]

Thus the *Mucor*-type of Life-Cycle emerges as a *two-phase* life-history,

[1] Reinke (1892), 'Atlas D. Meeresalgen', Taf. 35.

[2] For decadent coenocytic production of multinucleate spores of Mucorini cf. Harper on *Sporodinia*; Rei Progressus (1913), p. 529.

delimited by two resting-spores; one (the zygote) admittedly more adapted for endurance of extreme desiccation; the other, with more feeble vitality so far, but distinctly a 'spore' by organization, and now definitely adapted for flotation in damp air, as well as by water-carriage; the mechanism of discharge being still hydrostatic, and the spores liberated in fluid-masses. The alternation of generations need not be precise; but the biological mechanism is significant, and the two phases are each clearly delimited as an adaptation of the life-cycle of more elementary marine algae with sexual gametangia and unilocular sporangia (Ectocarpoid series); originally both equally adapted by their flagellated phases for dispersal in the aqueous medium of the sea.

From such a comparison of the Mucorini with more aquatic Phycomycetes, it is thus possible to obtain an idea of the problems of the new equipment required in the transmigration of the most simply organized filamentous forms; and it now becomes possible to map out the requirements of transmigrant saprophytic Fungus-phyla, and to apply them to the case of the more massive marine algal growths from which more massive fungus-somata may be derived; for example:—

(1) The filamentous hyphal mycelium may deteriorate to the coenocytic condition, with multinucleate segments, or of wholly non-septate organization; features which obtain in special cases of marine algae (Chlorophyceae and Florideae).

(2) Segmentation of mycelium, and abstriction of ramuli to free plankton-units ('Saproplankton'), may give a sprouting 'Yeast'-stage, as a new mechanism regressive for the special conditions of a nutritive solution demanding increased surface-area for metabolic exchanges.

(3) Similar ramuli may be abstricted as gemmules, to perennate with thickened membranes as *chlamydospores*, or be wind-borne as 'conidia' of sorts.

(4) Mass-aggregations of mycelium, similarly storing food, enduring desiccation, and perennating, give the case of 'sclerotia' and 'tuberous' formations.

(5) Sexual phases press to the limit of reproductive progression, from extreme heterogamy to oogamy, fertilization *in situ*, followed by loss of the flagellate-phase, with necessary siphonogamy; as also to 'conjugation' of imperfectly delimited sexual 'organs' (originally gametangia). A resting-stage for perennation is commonly intercalated in the zygote, in the case of filamentous forms; though this will not obtain in the case of a massive soma, in which post-sexual nutrition becomes available. All these factors, again, may similarly work out their progression in the case of higher land-flora, as also in starved transmigrant types of green algae of fresh water.

(6) The asexual organ (as unilocular sporangium) may be abbreviated to a mere 'conidium'; or may replace the flagellated units by 'endospores'; and these being air-borne will be modified to endure more or less desiccation.

(7) To this may be added the production of special ramuli, or branch-systems, elevating either conidia or sporangia above the substratum (as 'conidiophores' or 'sporangiophores'), the natural consequence of the utilization of subaerial dispersal.

(8) In relation to the degree to which cycles of sexual and asexual phases had been already attained in the algal life-history, these will become the more exaggerated under subaerial conditions. Each genus or group meets its own problems; and as is commonly the case in regressive marine algae of modern seas, the sexual phase may be entirely eliminated, following the deleterious effect of restricted autogamy. Single phases of a complex life-history may be thus isolated in response to special conditions of biological environment; decadence in the Life-Cycle being

again only another form of deterioration in the somatic organization, as the new source of food-material, often freely available without special trouble, cuts out any necessity for the mechanism which originally produced both the algal benthic soma and the value of the marine life-cycle.

(9) In all cases it must be borne in mind that, as the wastage of autogamous gametes is wholly compensated by *siphonogamy*, the more obvious morphological details of the sexual mechanism, other than that expressed in nuclear organization, may wholly disappear, without necessarily affecting the nuclear mechanism; though such deterioration of cell-mechanism does not necessarily imply 'loss of sexuality' in the strict biological sense.

(10) The function of dispersal still remains to be provided for, and this is relegated to the products of the asexual sporangium, the spore-output of which requires to be enormously exaggerated to compensate the new conditions of wastage of the air. Such sporangial stages soon begin to assume a much more prominent part in the reproductive life-history, and may, in fact, become relatively so predominant, that the sexual stages appear reduced, and even rare by comparison. Hence the story of the greater modern groups of larger terrestrial fungi is mainly made up of the consideration of 'sporophores', 'sporangia', and spore-output (much as in the case of higher Land-Flora, and for the same reason); while the whole life-work of the individual appears spent in the production of asexual spores. In this manner an entirely false impression may be created, owing to the insistence of this new problem of the wastage of the air-borne spore, which also tends to assume the perennation-phase, as the zygote passes on to a condition of post-sexual nutrition.

Beyond the Mucorini, as the key-group to the comprehension of the subaerial Phycomycetes, special interest attaches to three main phyla of existing Fungi, conveniently isolated as Ascomycetes, Basidiomycetes, and Uredineae; groups with no direct relationship, though attempts at 'linking' them in different hypothetical combinations have exercised the ingenuity of many botanists for the last fifty years. The special features of these great series may be briefly indicated:—

Ascomycetes. Though so generally constant in the details of the *ascus*-mechanism, with eight included *ascospores*, the great range of somatic type within the group precludes the possibility of the forms being merely the expression of special adaptations to subaerial conditions; and the alternative standpoint suggests that this great group represents the survival of a series of marine algae, otherwise unknown in modern seas, which had already attained a phyletic horizon, in some respects comparable with that of modern Florideae, before the transmigration took place. That is to say, it is to the more generalized, holo-saprophytic types of the group that one must look for the more primitive forms, and the full life-cycle; for example, to a massive land-growth as *Morchella*, rather than to minute holo-parasites as *Sphaeria*, or types commonly regarded as 'primitive', since apparently 'simple' in organization, as in the case of minute leaf-parasites as Erisypheae and *Sphaerotheca Castagnei*. The latter, as a holo-parasite on photosynthetic leaf-laminae of higher plants, has no more claim to be regarded as 'primitive', because its ascocarp is limited to one ascus only, than such a minute epiphytic *Chantransia*-form as *Kylinia rosulata* (Rosenvinge, 1909), with cystocarp of 2–3 carposporangia, would pass as a 'primitive', since minutest, Floridean.

Consideration of the typical life-history shows the general equipment of a 'two-phase' life-cycle, though much obscured by secondary deterioration in the sexual phase, and by new subaerial adaptations in the asexual phase, is still recognizably algal and benthic; though as previously indicated, with no possible connexion whatever with that of modern Florideae, still expressing suggestions of convergence in several important respects. Apart from the great range

of somatic organization (cf. *Xylaria*), accessory means of propagation ('conidial' stages, as in *Penicillium*), and perennation (chlamydospores, and sclerotia as in *Claviceps*), reproductive organization follows a simple two-phase cycle, including phenomena of sexual fertilization and meiosis (Clausen, 1909), as also haploid and diploid phases, entitled to the nomenclature of 'gametophyte' and 'sporophyte' if so desired; though these terms may with great advantage be wholly scrapped. The essential point to note is that fertilization *in situ* had passed on to the development of a parasitic diploid phase, nourished at the expense of a massive, persistent, gametophyte-phase, somewhat in the manner of the Florideae, apparently before the plants had left the sea. Flagellated phases have been similarly wholly lost, and fertilization by siphonogamy (*Pyronema*) may conceivably give place to a new type of spermatogamy (*Collema*, &c.) in which the male conjugation-tube is abstricted as a free 'conidium'-like 'spermatium', while the female conjugation-tube is raised to the dignity of a so-called 'trichogyne'; the process bearing no relation to the normal details of spermatogamy among the marine Florideae, and all limiting terms of abstricted units being alike in their homologies as abstricted rudimentary 'ultimate ramuli', though affording a suggestive attempt at securing allogamy.

The reduced and parasitic diploid phase, again, may be protected and fed, by special developments of the parental tissues (mechanism of ascocarp or perithecial 'wall', 'paraphyses', &c.), also similar in biological function to the 'cystocarp' of the Floridean, though wholly different in detail; ultimately the vestigial and filamentous sporophyte produces asexual reproductive organs as unilocular sporangia including phenomena of meiosis, but continuing to three mitoses in all, or a limiting case of *eight* ascospores; again in a manner fundamentally distinct from the carposporangium of modern Florideae (in which the end-ramuli now appear as monosporangia which do not initiate the meiotic process), though running curiously parallel, so far as the nature of the nuclear divisions is concerned, with the female gametangium of the Fucaceae.

Beyond this algal horizon, however, the essential feature is the maturation of wind-borne spores, with protective exosporium, *within the ascus*, more in the manner of the Mucorini; and the dehiscence of the ascus to set them free in damp air similarly involves hydrostatic pressure and the discharge of wet spores. In connexion with the dehiscence of the ascus, thus homologized with the unilocular sporangium of the sea, it is interesting to note (cf. Buller,[1] 1909, p. 236) the fact that the mechanism of ascus-discharge may involve an upward projection of the ascospores for a possible distance of 2–3 cm. from an exposed hymenium, with the mechanism of propulsion little changed from that of *Laminaria* discharging motile zoïds in sea-water. The ascospores are thus originally emitted in sub-saturated air, and prove sufficiently successful for wind-flotation, as also for washing-off and flotation by the presumably older method of atmospheric precipitations. Following the immediate parasitic development of the zygote, the unicellular, perennating, 'encysted' unit, as well as the dispersal function, is thus provided for at the ascospore-stage, to which gametophytic conidia may appear as a secondary detail; the latter being apparently always of the value of abstricted end-ramuli, than reduced sporangia themselves, and produced as a concession to the wastage-problems of new and special conditions of life (cf. *Claviceps*).

In dealing with all such highly-specialized and heterotrophic organism, it is impossible to regard any life-history from a simple academic standpoint; all the factors of the special mode of life must be taken into consideration, as bearing on extreme phases of specialization; since these will obviously become the more extreme as the conditions of life are the more complex, in the case of organism struggling to survive in phases of secondary and even tertiary dependence. Thus while heterotrophic forms living in decaying vegetable matter are to begin with

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[1] Buller (1909), 'Researches on Fungi'.

plant-phyla *in extremis*; much more so are hemi- and holo-parasites, restricted to ultimately a few hosts, the latter again possibly limited in their activities by seasonal and climatic factors. An epiphyte on an epiphyte is rare even in the sea; still more will a *parasite on a parasite* express the limiting case of somatic deterioration, and a range of extreme special adaptations, if it is to remain efficient, that is to say, living and reproducing successfully. Among holo-saprophytic subaerial forms, the intensity of the wastage is again reflected in the enormous extension of the hymenial region and spore-output (Apothecia, *Peziza*-type); the hymenium may become convoluted (*Morchella*), or still more elaborately organized in subterranean forms (*Tuber*); on the other hand, restriction of the hymenium to a few asci only (*Erysiphe*) is associated with a reduced completely parasitic habit, seasonal periodicity, and the utilization of special hosts, as also with a further extension of the abstriction-mechanism to a conidial phase. The case of the omnipresent *Penicillium*, again, may be instanced as an illustration of one of the limiting terms of extreme reduction—specialization in a modern subaerial type; and though the sexual phase may be cut down to obscure limits, the general acceptance of the ascus-stage as always presenting meiotic phenomena implies that a sexual and nuclear fusion must take place at some point, though reduced to the conjugate habit of closely associated nuclei (pseudogamy); while the wastage- and dispersal-problems are more immediately compensated by secondary conidial formations.

Though the association of the Ascomycetes with marine Florideae may appear wholly preposterous, and the expression of an entire lack of perspective in dealing with the reproductive processes of the vegetation of the sea; the degree of physiological convergence in the more fundamental aspects of (1) fertilization *in situ*, (2) the parasitic diploid phase, continuing as an asexual and alternating generation, is so remarkable and unique, that it is still possible to suggest the association of Ascomycetes, as a class, directly with somewhat similar marine algae, now wholly unrepresented in the sea, but of a horizon much earlier than that of modern Florideae; as dating to a time when the diploid parasitic carposporophyte of the latter still presented meiotic divisions in its unilocular sporangia, and the life-cycle was still 'two-phase' in type; i.e. not as yet extended to the more typical 'three-phase' cycle of the modern Florideae.

On the other hand, while the connexion of the Ascomycetes with modern Florideae may be thus only very remote, it is interesting to note that the analogy of the latter group, in its complete isolation, may be utilized to press the moral of the independent nature of this Fungus-phylum. The remarkable dominance of the 8-spored ascus equally expresses the complete isolation of the Ascomycetes in the Fungus-series. Its origin is clearly to be sought independently among the Algae of the Transmigration; and there is again no connexion whatever, for example, discernible with such a group as the Mucorini; though certain phases of special subaerial adaptation may again run very parallel. Other phenomena similar to those obtaining among Florideae may be also expected to obtain. Phases of the life-cycle may be omitted ('Fungi imperfecti') in the case of decadent forms of the more inferior stations, sexuality and meiosis may be wholly eliminated; the race continuing to exist in the last resource by conidial developments alone, just as Floridean types may be reproduced solely by tetraspores or monospores (*Rhodochorton* and many Chantransias), in smaller forms, or even in larger types, as in the case of *Rhodymenia palmata*. Academic views of phyletic connexions with other main series of the Fungi may be wholly scrapped; and no view of the Ascomycetes and their origin, which does not face the problem of transmigrant subaerial existence, the evolution of the air-borne spore, and modes of perennation in absence of casual water-supply, can have any satisfactory bearing on the subject. The group remains, in its special transmigrant aspect, as entirely isolated, in a manner now beyond recall. The case of remigrant, minute, parasitic types, found growing on sea-weeds, as *Mycosphaerella Ascophylli* and *M. Pelvetiae*, adds but another link to the study of the vicissitudes of the transmigration

of a type of vegetation quite as unique in its secondary heterotrophic habit as a race of holozoic (animal) organism.[1]

Basidiomycetes. To this vast series of Fungi, equally narrowly circumscribed by the possession of a special reproductive organ as a 'basidium', normally producing four 'spores', all preceding generalizations, based on the progression of the Ascomycetes, apply with increased force; and no presentation of this group can be accepted which does not similarly take into account its direct origin from some group of transmigrant and similarly saprophytic marine algae, passing on in parallel series to similar problems of massive saprophytic somatic organization on a substratum of decaying plant-débris; readily passing to immediate saprophytism on dead plant-tissues, and ultimately holo-parasitic on forest-trees; attaining full variety and scope in the undergrowth of tropical forest-association, with the massed food-material of decaying tree-trunks[2] (Beebe, 1917). Hence less insistent possibly in the expression of perennation-phases enduring extreme desiccation, though similarly solving all the problems of the air-borne spore, wind-dispersed and more successful, though on lines wholly distinct from those of the Ascomycete; and in the highest types even attaining a mechanism of insect-dispersal,[3] with associated 'scent' and attractive colouration, in the quiet environment of lower forest-levels; a few examples of which extend to the Temperate zone (*Clathrus*, *Phallus*) to give a slight idea of the limiting terms of this wonderful exhibition of saprophytic life, perhaps the most widely divergent from the conventional idea of what a 'plant' should be. Hence the Basidiomycetes are commonly accepted as the most fungoid of the Fungi, and the most advanced of the Eu-mycetes; since in them all the secondary subaerial specialization of the Fungus-type of organism reach their optimum expression; even though the group need not express the most complex life-cycle, and remains at a 'two-phase' horizon. Similarly, though the original evolutionary attitude of subaerial botanists tended to link all these forms within one Fungoid series, and to construct a connected scheme, more or less as a convenient convention, from the simpler Phycomycetes to the higher Basidiomycetes (De Bary); these speculations necessarily entirely ignored the marine origin of all such land-types; and, in view of the reality of the probable progression, such academic views of so-called phyletic systematy as have been widely accepted on the authority of Brefeld, appear threadbare and futile, as again mere historical curiosities of the science.[4] As in the case of the Ascomycetes, it is to the more generalized

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[1] The case of Lichens, omitted for the present, though of greatest interest in that *intrusive* algal organism enables the saprophytic type to retain much of its original somatic organization, as centric ramuli, or dorsiventral and bilateral constructions: the value of the 'symbiosis' being again interpreted from the standpoint of the general phenomena of such intrusion in marine organism.

[2] Beebe (1917), 'Tropical Wild Life in British Guiana', 'accumulated débris of centuries and fallen tree-trunks . . . Fairy castles, laces, sunshades, pikes, spears, pagodas, spirals, and scores of other forms of fungi for which no simile existed' (p. 83).

[3] 'Brazilian Pilzblumen', Möller (1895); Bot. Mitt. aus den Tropen.

[4] Empirically selected details of reproductive mechanism, and a few sketchy diagrams of the septation of reproductive organs are often regarded as sufficient to afford a basis for the consideration of the origin of entire races, in complete ignorance of the full life-cycle, as also ignoring conditions of growth and somatic organization, as the equipment of the race in meeting the more insistent problems of all grades of saprophytism, as well as extreme parasitism, on the aerial portions of seasonal vegetation. The so-called 'Brefeldian System' of Hemibasidii and Protobasidiomycetes may be wholly rejected as non-illuminative, and serving no useful function beyond mere classification; but rather tending to obscure fundamental factors. To consider, for example, the massive perennial growth of Polypori, 2–3 ft. in diam., or free organism living wholly in soil (*Agaricus*, *Lycoperdon*), as ever

and massive types of the forest-bottom, or open prairie-land, that one must look for the original definition of the race. Forms with continuous growth, as expressing abundant food-material and indefinite time, as in the case of forms living on decaying arboreal vegetation at the base of a tropical forest, may be in all probability regarded as the lineal descendants of the original transmigrant organisms in the primary condition of the race.[1]

The wastage coefficient of air-dispersal is characteristically counterbalanced by an enormously extended hymenial layer, lining 'gills' or 'pores', and constituted essentially by 'basidia' in which meiosis is apparently normally effective, giving nuclear divisions restricted to those of a single tetrad.[2] This expresses the fact that the basidium is to be regarded as essentially a 'unilocular sporangium'; so far comparable, though by no means identical with, an *ascus*, or even a *teleutospore*, in that all these last may at bottom be regarded as similar asexual organs.

New departures are strongly emphasized: the fact that meiosis is interpolated in the basidium apparently affords the clue to the reproductive organization, as expressing the fact that somewhere in the antecedent life-history a nuclear sexual fusion may be postulated, even if no more than the approximation of conjugate nuclei; and thus indicative of a life-cycle of two phases, on the general plan of the Ascomycete, though so different in secondary details of subaerial equipment. With no differentiation in the zygote, the problems of perennation and dispersal are similarly centred on the basidium-mechanism; and in response to the enormous wastage of subaerial dispersal the spore-output is enormously exaggerated; while special adaptations to minimize such loss become again the criterion of chance of survival, and a higher grade of organism. The key to the subaerial advance of the Basidiomycetes is thus to be looked for in the characteristic details of the basidium, and the mechanism of spore-discharge, as expressing an advance on the corresponding phenomena observed in the case of the Ascomycetes; in that—

1. The basidium, restricted to a nuclear 'tetrad', expresses an ultimate phase of reduction beyond the eight spores of the ascus.

2. The essential point is that the basidium-sporangium no longer dehisces; and the spores are no longer discharged in damp air by the effect of hydrostatic tension.

3. The basidia are again normally so orientated that the spores fall vertically downwards (i.e. in all well-differentiated *Agaric*-types and *Polypori*) and have so far lost connexion with chance flotation by rain-water.

4. The mechanism of discharge is active; the spores being propelled for short distances (0·1 mm., Buller); and the four units are discharged serially and independently, by an adoption of a mechanism of conidial abstriction.

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evolved from minute holo-parasites of green foliage-leaves of the type of the Uredineae or even *Exobasidium*, from mere details of the little-understood basidium, whether septate or non-septate, is beyond serious discussion.

[1] It is interesting to note that alga-like growth-forms are more conspicuous among earlier Basidiomycetes of massive build than in any other fungoid alliance. It is for example impossible to regard such widely divergent growth-forms as the *Xylaria*-like *Polyporus squamosus*, figured by Buller (1909, p. 58), or *P. frondosum* (Hennings, 1898, p. 116), the Cauliflower-like *Sparassis ramosum*, over a foot in diameter, the pagoda of *Mycodendron paradoxum*, or the branching systems of many Clavarias and Lachnocladiums, as being in any way the response to special conditions of a saprophytic mode of life; although they may be decadent and vestigial variants on more algal somata. For so-called fungus-types among sea-weeds cf. *Melobesia* (*Lithophyllum*) *lichenoides* and *M. agariciformis* of the Phyc. Brit. t. 73. An unfortunate obsession that the mycelium of a fungus is the *soma*, and not the sporophore, is on a par with the equally fatuous suggestion that a moss-protonema is the gametophyte, and the leafy shoot only the 'archegoniophore' (cf. *Rafflesia*).

[2] Guilliermond (1913), 'Rei Progressus', p. 472.

5. The basidiospores dry quickly (in a minute or so), and acquire a special biology in virtue of their small size (averaging 10 μ diam.), passing off with a smoke-effect, and attaining a limiting velocity of as little as 1 mm. (–5 mm.) per. sec. (Buller, 1909).

6. Accessory conidial stages are rare, and the output of basidiospores may be taken as the general wastage-coefficient. According to Buller, a common Mushroom (*Psalliota campestris*) may discharge 1,800 millions per sporophore, at a rate of 40 millions per hour: *Polyporus squamosus* 10^{11} spores per annum; and an extreme case of *Lycoperdon giganteum* 7×10^{12} of 10 μ spores from one fructification, as possibly the record, so far as known, for the vegetable kingdom; at any rate far beyond anything known in the case of marine algae (cf. *Saccorhiza*); i. e. a record in units, but not in mass of material.

Without going into further details at this stage, it may be pointed out that the 'septate' basidium does not occur in the case of any type with special claim to be regarded as 'primitive'; a vast range of imperfect, rudimentary, and regressive forms need not be accepted as elementary, merely because they are small and their life-cycle ill-defined; while the most remarkable advance is that of those types which in the depths of the tropical forest pass on to relations with insects in which dispersal by such agency replaces the action of the wind, exactly as the same progression has been carried out in the case of higher entomophilous Angiosperms, with a degree of biological parallelism which is at times astonishing.

Uredineae. While both Ascomycetes and Basidiomycetes, though clearly sharing many of the essentials of the equipment and its consequences of more massive marine phytobenthon, can be referred neither to any existing algal series, nor to any direct relationship with each other, a critical interest attaches to the relatively small holo-parasitic series of the Uredineae, which have been variously regarded as possibly associated with either or both these preceding groups, or even as intermediate between them (De Bary); while in recent years they have been freely accepted as 'Proto-basidiomycetes' on the dubious authority of Brefeld. As in the case of the leaf-parasites of the Ascomycete series, it is impossible to regard such minute forms, holo-parasitic on the highest types of land-vegetation, on the actual photosynthetic tissues, as in any sense primitive. The last fact sufficiently indicates that their somatic deterioration will be of an extreme nature; while the fact that their hosts, often more than one, are also subject to the vicissitudes of climate and extreme seasonal periodicity, sufficiently expresses the suggestion that their reproductive specialization will be also of the most extreme kind; in that wastage must be more insistent as the problems of dispersal and migration increase; e.g., with the difficulty of finding the necessary host when the latter ceases to be a common plant. The same generalizations apply to the case of all fungoid leaf-parasites, which tap the food-supply of the host at the source; though, as in the case of the Uredineae, not necessarily intracellular; just as the limiting phases of animal parasitism are found in organisms living in the blood of higher mammalia. Great developments of the conidial spore-stages in such forms are to be normally expected; and in such organism, at the limit of somatic deterioration and reproductive specialization, 'primitive' factors are to be looked for, more particularly, in the fundamental mechanism of the life-cycle.

Taking again the accepted type of such organization as represented by *Puccinia*[1] and *Phragmidium*[2], the life-history presents distinct evidence of at least a 'three-phase' cycle; and when the subject is freed from obsession in favour of the essential morphological value of haploid and diploid phases, these reduce to a very simple scheme, very comparable with that of the Florideae in many respects, though again divergent in some important details. Alone of all existing forms the three-phase life-cycle of the Florideae, attained in the sea,

[1] Blackman (1904), Ann. Bot. xviii; (1906) xx.
[2] Christman (1907), Bot. Gazette, 44.

affords the clue to that of the Uredine, though with vague possibility of phyletic connexion. The three-phase Floridean is again the expression of a state of affairs beyond that of the two-phase *Dictyota* and the ancestral condition of the Ascomycete, Basidiomycete, and even Archegoniate phyla, as following up the consequences of the utilization of apogamy and asexuality in marine phyla, in which such phenomena were primarily evolved. The Basidiomycete, as already noted, presents a two-phase type of life-cycle, but is significant as affording a view of the mechanism of initiation of conidial extensions from the tetrad units of the tetrasporangium (now a basidium), very much in the manner of the production of sporidia from a germinating teleutospore of the Uredine; but clearly in an entirely distinct phylum, and so far biologically convergent as the expression of adaptation to similar conditions of environment, and the demand for air-borne spores with a minimum of trouble in production.

Taking the stages of the Life-history as typically illustrated by the familiar *Puccinia* forms, step by step, the story runs intelligibly clear on the lines of the full Floridean type, though with further phases of deterioration :—

(1) The parasitic endophytic mycelium, with sexual organs deteriorated to the ultimate stage of siphonogamic conjugation, and even nuclear approximation as delayed nuclear fusion, conceivably follows on after vestigial spermatogamy of a stage beyond that of the Floridean, again, in that the antheridial ramulus is itself abstricted, rather than slipping the antheridial contents. The result of such inevitably autogamous sexual approximation is—

(2) a parasitic attached 'diploid' zygote, a holo-parasite on a holo-parasite, developing in the manner of a carposporophyte, and thus doomed to a limiting condition of starvation, as the *Aecidium*-stage; of further interest as compared with that of the Floridean, in that protective adaptations are provided at the expense of the second individual (peridium) by undoubted phenomena of 'sterilization'. This carposporophyte instead of liberating even monospores, as representing the suppression of meiotic tetraspores; again, as in the case of the antheridium, abstricts segments of the ultimate ramuli (carposporangia) bodily in series, by an ingenious mechanism of 'intermediate cells'; thus providing for the serial and successive output of a distinct *conidial* formation; and meiosis is delayed over the second generation. On the other hand, as in the Florideae, a dispersal mechanism of free spores is provided, this being the main point; though now air-borne, and even perennating, as *aecidiospores*.[1] The nutrition of a holo-parasitic carposporophyte on a parental holo-parasitic mycelium, which in turn lives on the photosynthetic tissue of a green leaf, itself presenting excess production of polysaccharide (starch), as an indication that it is insufficiently supplied with nitrogen from the roots, involves the difficult point as to what may be the nitrogen-prospects of such a carposporophyte. There is thus ample suggestion of the reducing-effect of sheer proteid-starvation; and one begins perhaps to get a rough idea of what may be the struggle for life of such a highly specialized fungus of the present day, so far from the primal sea.

(3) The succeeding individual, again diploid, in the manner of the Floridean,

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[1] The term 'generation' is used in its original significance, as expressing the period of a single life, beginning with a uninucleate spore, as a single cell, and ending with the production of a similar unicellular 'spore'-unit. Owing to an unfortunate obsession as to the significance of haploid and diploid mechanism, initiated by Strasburger (1894), the term 'generation' has been applied to a cytological state (cf. Bower, 1919, 'Botany of the Living Plant', p. 482). The expression *phase* may be used as an alternative. For example, the Life-history of a Floridean, of higher grade, involves three distinct *individuals*, one being parasitic, and is definitely 'three-phase'; apart from any question as to the number of chromosomes in the nuclei. To regard 'cytological generations' as more fundamental than morphological differentiation of individual lives is purely academic, as a concession to the mysteries of Cytology; it confuses two distinct phenomena, rather than affording any broader outlook on plant-life.

is free, so far as its direct parasitism on the green tissues of the leaves of another host is concerned, and it repeats the diploid asexual phase, again producing potential unilocular sporangia. In these, in turn, meiosis is inhibited; and the sporangium is abstricted as a whole, at an early stage, as another conidial form (uredospore), to repeat the process indefinitely if conditions permit. Or this stage is brought to an end by similarly deteriorated (if juvenile) perennating sporangial ramuli, not definitely abstricted, and often formed in series (*Phragmidium*) which remain connected. So far the third individual has delayed meiosis; though again giving the possibility of dispersal, and again subject to an enormous coefficient of wastage.

(4) On germination of the teleutospore, however, meiosis is as it were grudgingly effected, following an antecedent completed sexual fusion, and a resultant tetrad of four nuclei alone remains to express the lost stage of the tetraspore; the four nuclei being now utilized, much as in the Basidiomycete basidium, to constitute the nuclei of conidial ramuli, themselves really the laterals of the most microscopic parasitic individual conceivable; and really a fourth individual holo-parasitic on the contents of the teleutospore. Meiosis, that is to say, is theoretically interpolated at the germination of the fourth individual of a four-phase sequence; and the miniature ramuli are again abstricted as conidial stages (*sporidia*), utilized for air-borne dispersal.[1]

Parasitic offspring on parasitic parent, malnutrition, starvation for want of food-salts, and the nitrogen-problem, though soluble carbohydrate may be cheaply obtained from the excess of the host, are the determining causes in this complex life-history, as expressing the limit of adaptation to starvation-effects in the vegetable kingdom; a little physiological consideration of the problems of such evolution is more convincing than academic morphological conceptions of the value of haploid and diploid phases. It must be remembered that Fungi are not high-grade organisms utilizing sexual reproduction for the improvement of the race, as leading to higher forms of plant-life, but autogamous starved organisms, living as best they can, under conditions remote from those for which their organization was originally the response; doomed to progressive wastage under competition with higher types, and making the best of the very feeble equipment with which they left the sea; while once the mechanism of the autotrophic soma is lost, there is no chance either of recovery, or of the initiation of a new one; all primary factors of the benthic soma being marine in origin.

Whether these generalizations are wholly satisfactory or not, in view of present knowledge of the groups, does not affect the present question, that (1) a thorough knowledge of the fundamental equipment of marine algae is the essential feature of any phylogenetic discussion of the evolutionary progression of land-Fungi; (2) the subject is put in an entirely new and intelligible light when considered from the standpoint of the parallel progression of several distinct algal phyla; rather than attempting to build up *de novo*, on no satisfactory basis whatever, speculative views of the elaboration of a massive soma, and complex phases of life-cycles from the merest elementary filamentous or coenocytic Phycomycetes; as if Fungi were monophyletic, and stood complete within their own domain from the beginning, or all the way back to the condition of flagellated plankton. In the present state of their complete isolation, as a few surviving residual phyla of lower organism, it is futile to attempt to 'link' any fungus-series with any known algal alliance; yet at bottom the broader generalizations as to the fundamental equipment of morphological, anatomical, and cytological mechanism of types in the unchanged medium of the sea, must constitute the foundation on

[1] Grove (1913), 'British Rust Fungi', p. 27, naturally gives the academic theory of the intercalated dipliod sporophyte, though vague on the tetraspore 'mother-cell' (p. 28, *Corallina* (p. 37), and arrives safely at the conclusion that the Uredineae do not represent any stage in the evolutionary story of the Basidiomycete: cf. p. 82 for Florideae.

which all considerations of the evolution of land-organism must inevitably be based.

With even such a brief review of the leading types, the moral of the Fungus-series should be sufficiently clear. While all the groups are to be considered from the standpoint of the progression of heterotrophic nutrition in transmigrant phyla of once marine algae, the series remains a collection of remarkably large and isolated groups with no direct relation to one another, or to any modern algal forms, with no known beginning and no definite ending, often diverging widely in initial equipment, as expressed more particularly in the phases of the life-cycle. Yet all are seen to have progressed along the same path, and are so far convergent in their secondary departures; though presenting a range of type and secondary equipment which affords the basis for the consideration of what the transmigration really means, as the same factors work out in such different series, with varying degrees of success, according to the physiological horizon attained before such transmigration began. That is to say, the same effect has been worked out simultaneously in many distinct algal groups, all so far running parallel in the successful assumption of heterotrophic nutrition; though so far again to be regarded as the expression of failure from the standpoint of autotrophic vegetation. Such phenomena afford the clue to what may be looked for in the case of the more dominant and successful autotrophic types of land-flora. All transmigrant phyla have been through the same experience, with more or less success. There was only one way from the sea to the land, solving successively all the problems of the new subaerial environment; though many types still existing have solved a part of the problems, and so survive as partial failures to demonstrate the path of the progression.

Summary. (Fungi.)

(1) The great series of the Fungi has been often vaguely taught, and with difficulty appreciated, for want of some definite standpoint with regard to the meaning of their progressive evolution. De Bary, apparently, could see little in them of theoretical interest beyond the progressive deterioration of sexual processes (assumed originally perfect from the analogy of higher land-plants and animals); while Brefeld's view, beyond obscuring sexuality, centred mainly in an academic distinction between 'conidia' and 'sporangia'. It is hoped that the view put forward in these pages, of regarding them solely in the light of saprophytic and transmigrant derivatives of marine algae of higher grade, may afford a more promising clue to their special peculiarities.

(2) Given the initiation of sexual fusions, and the consequences, as a means of improving the race, in virtue of mingled nucleo-plasm and the chances of variation following from meiosis, it has been shown (elsewhere) that the great factors in counterbalancing the inevitable wastage of these reproductive processes, in marine phytobenthon of the moving sea, may be included under the three headings of *asexuality*, *heterogamy*, and *fertilization in situ*.

(3) To these the transmigration to subaerial conditions adds the necessity of *perennation*-phases, enduring casual desiccation, intercalated in one-phase cycles at the stage of the zygote (which is hence said to 'rest'); since the sexual organs, themselves primarily the response to unsatisfactory conditions of environment, represent failing somatic units.

(4) But given a massive thallus, the attainment of fertilization *in situ*, and consequent loss of the dispersal-phase of the motile gametes, post-sexual

nutrition of the zygote supervenes, and the perennation-phase is passed on to the spore-stage of the succeeding sporophyte; these also take on the necessary function of *dispersal*, whether set free in the moving medium of water, or liberated to be carried by air-currents. In all cases the adaptations to secure a minimum of wastage, in these phases, afford the clue to the evolution of higher organism of such special grade, as they also become the measure of the success of the type.

(5) *Hence transmigration can be only fully effective in an algal group which has already differentiated a two-phase life-cycle, following a massive somatic organization.* As the wastage of the sexual phase is counterbalanced by fertilization *in situ*, the burden of the new problems falls on the *asexual units of the unilocular sporangia* of the parasitic sporophytic phase. Similar deductions may be applied to higher grades of more successful autotrophic organism. The special biological interest of the Fungi centres in the fact that, owing to the adoption of an entirely new mode of heterotrophic nutrition, the insistence of new problems can be traced quite independently in the reproductive organization. The new factors of wastage being isolated under the terms '*perennation*' (as response to the chances of loss of casual water-supply), and '*dispersal*' (as relating to the substitution of the agency of moving air for the older medium of moving water).

(6) Debarred from any remarkably new departures in somatic organization by the consequences of the heterotrophic habit, as destroying the original mechanism devoted to photosynthetic metabolism; the special value of the Fungi, as transmigrant to subaerial environment, may be traced in the polyphyletic and manifold evolution of the *air-borne spore* from the unilocular sporangium of algal forms; the latter passing through all stages of progression, from production of the original flagellated units, discharged by hydrostatic mechanism, to the phase of the immotile 'spore'; as also to all stages of the monosporangium, detached as 'conidium', and even attaining the extreme condition of insect-dispersal. In all cases the spore-stages (with few minor exceptions, as the septate spores of many Ascomycetes, and the large zygospores of Mucorini) retain with remarkable unanimity a general approximation to the 10 μ value, still obtaining in the metabolic units of marine algae. In this way, without much straining, a lineal progression may be traced from the flagellated phase of the plankton of the sea to an equally minute 'plankton' of the air, floating as omnipresent and invisible dust of living organism.

X

BRYOPHYTA

GREATER interest attaches to more definite autotrophic Land-Flora, of which the surviving types are classed as Bryophyta and Pteridophyta. Beyond the latter the attainment of the seed-habit marks the culmination of the dominance of subaerial conditions; the necessity for any external source of water in reproductive stages being successfully eliminated from the life-history. But so long as an external medium is required for the flagellated plankton-gametes, the transmigrant condition remains in evidence; and Bryophyta and Pteridophyta conventionally include all the phyla of the transmigration-period which have survived the natural selection of this

epoch without having attained to the still higher phase of the seed-plant, as the Cryptogams of older systematists. So far as the attainment of the dominion of the land is concerned, the Bryophyta can be only regarded as failures, frankly vestigial, and off the main line of higher evolution, though widely divergent from any original condition of transmigrant algae. The suggestion has been previously put forward, that this follows naturally from the fact that they are wholly unable to initiate a root-system beyond the condition of attachment rhizoids; the latter fact in turn sufficiently indicating that they had in the aquatic benthic phase no better hapteron-mechanism, and were thus unable to initiate one. The consequences are seen in the extreme depauperation of the soma as soon as it emerges from the water. Only one main type can compare in somatic organization with an average sea-weed,—the more or less submerged bog-moss *Sphagnum* (6 ft.), though the submerged *Fontinalis* may also attain considerable dimensions, and curtain-masses of Jungermannias are described for tropical rain-forests of the Andes (Spruce: *Bryopteris*, *Frullania*).

That the centric type of the Moss with multiseptate (parenchymatous) cell-construction, ramification, leaf-members in a distinct rhythmic phyllotaxis-pattern, and a definite system of apical growth, expressed in the serial segmentation of a three-sided apical cell, which also controls the sequence of the leaf-members and branches, is to be regarded as the primitive stage, obviously follows from the standpoint that all these factors are the product of conditions of marine environment in marine phytobenthon. On the other hand, the view that the most inferior dorsiventral types of Ricciaceae are to be regarded as the elementary progenitors of the race, has been so curiously persistent in botanical literature for the last fifty years, that it can be only regarded as a historical curiosity of the science, originating in perverted pre-Darwinian lines of thought. The dictum that 'all dorsiventrality is secondary' has been ably upheld by Bower (1908, p. 216) for Pteridophyta; as it is equally obviously the case in marine algae; the application of the same standpoint to Bryophyta follows naturally. Yet so insistent is this archaic view, that theories of the progressive evolution of the 'Leaf' have been traced from lateral lobes of the dorsiventral thallus of *Blasia*[1] and bilateral Jungermannias, as stages antecedent to the evolution of the leafy shoot of a Moss; regardless of the fact that the initiation of a centric mechanism, spacing leaf-members in a Fibonacci sequence is much more difficult to account for than mere dorsiventral lobing, and that every series, however plausible and attractive, can be read the other way.[2] That Jungermannias admirably illustrate the progressive dorsiventral bilaterality and reduction of the leafy shoot to the mere thalloid condition of *Pellia*, is the more obvious mode of correlating these facts; and as already noted it is to *Sphagnum*, with its highly differentiated shoot-system of leaves, branches of different categories, and apical cell-construction, that one must look for structural factors comparable with those of marine algae. (Cf. *Dasya Hapalathrix*, Floridean, 6 ft.; *Sargassum* with leafy shoot-system, 6 ft.; species of *Cystophyllum*, 6 ft., as comparable forms.)

[1] Cf. Cavers (1910), New Phyt., p. 229, for interesting phylogenetic tree, tracing *Haplomitrium* from *Pellia*: p. 225, 'Leaves have been evolved independently in several distinct phyla of the Anacrogynae': loc. cit. (1911) p. 41, for traditional descent of Bryales through *Jungermannia* to *Riccia*.

[2] Tansley (1907), New Phyt., p. 33, traces the frond of a fern from the 'dendroid' and dichotomous dorsiventral shoot-system of *Blyttia*, *Symphogyna*, and *Hymenophyton*: also able to conceive that Lycopods have been derived from a *Blasia*, *Fossombronia*, *Calobryum*-series (!).

So far as *somatic organization* is concerned, the great majority of Bryophyta are inferior to the highest expression of marine benthon; their most deteriorated forms are on a level with dorsiventral and prostrate sea-weeds; even the most elegant of the *Jungermannia*-series are less wonderful as morphological constructions than the thallus of *Leveillea jungermannioides*, or the miracle of *Claudea* among the Florideae, or even *Zanardinia* among the Phaeophyceae. Advancing specialization, as adaptation to a better type of photosynthetic environment, may be traced in the *horizontally* extended leaf-laminae of the larger Mosses (as in the assimilatory lamellae of *Polytrichum*), as also in the more definitely conducting tissue of the main axis.[1] But the leaf-laminae are still in the condition of bilateral 'ramuli', formed or controlled by the segments of the three-sided apical cell, in the manner of Rhodomelaceae rather than that of the Cystoseiras and Sargassums. The three-sided apical cell is again only intelligible as a segmentation mechanism, initiated in multiseptate algal organism, as a limiting case of centric organization (Fucaceae).

The *sexual reproductive organs*, as previously indicated (Chap. III), present fundamentally a combination of the factors of *Chara* and *Dictyota*; the massive microgamete-tissue being the expression of the transmigration factor of a single layer of protective cells over the gamete-primordia; the latter being so far 'immersed'. The relation of the archegonium to the antheridium summarizes the working out of advanced oogamy and fertilization *in situ*, in a manner common to all transmigrant 'Archegoniatae', and apparently inevitable. Both antheridia and archegonia are clearly based on 'ultimate ramuli' of multiseptate construction, which may bear in larger forms a definite relation to the leaf-arrangement (*Polytrichum*, *Sphagnum*), in the manner of the gametophores of *Sargassum*; or in the limit of reduction they are aggregated in one sorus at the apex of the shoot. With ultimate loss of leaves they may be left with purely chance arrangement and further immersion[2] (*Pellia*). The limiting type of such continued immersion in a dorsiventral thallus (*Anthoceros*), is of interest, because it is so closely paralleled by convergence in Pteridophyta (cf. *Ophioglossum*); types in which only the wildest imagination could trace any suggestion of direct affinity (Campbell).[3] In most cases the association of such ramuli with 'trichome derivatives' as 'paraphyses', is of further interest, as affording a glimpse of an older phase of the retention of ramuli of the 'filamentous soma' general among Phaeophyceae. So far as the gametophyte is concerned, the Bryophyta are types of purely deteriorated algal nature, however much they may appear advanced by the side of the residual Chlorophyceae of fresh-

[1] Tansley and Chick (1901), Annals Bot. xv, p. 32.

[2] For the suggestion that the Hepaticae may be fundamentally independent of the Bryales, since the antheridial and archegonial ramuli of the latter alone grow by a segmenting apical cell, cf. Cavers (1911), New Phyt., p. 44: the evolution of the archegonium, that is to say, being polyphyletic even within the group of the Bryophyta, and thus convergent in many transmigrant races.

It may be also pointed out that the recognition of antheridium and archegonium as 'ultimate ramuli' of a parenchymatous soma, and not mere 'trichome'-vestigia, suffices to imply that, in that such ramuli retain a simple centric organization, the thallus on which they are borne was also originally *centric*; and dorsiventrality has been secondarily attained.

The same would apply, however, to the attainment of the dorsiventral habit in the photosynthetic soma before the organism left the sea; just as many Florideae (cf. *Dasya*) still retain indefinite tufts of centric reproductive ramuli on bilateral fronds.

[3] Campbell (1911), 'Eusporangiata', p. 210.

water.[1] The antherozoid is so far identical with that of *Chara* (*Sphagnum*, *Pellia*) in all details (Guignard)[2], that there can be no doubt that *Chara* is a near representative of a still older filamentous stage of the green algae from which the transmigrants took off; though the gametophyte details only cover the smaller half of the story. On the other hand, the absence of a resting-stage, intercalated at the zygote (as in *Chara*), shows that the 'germination' of the oospore and the growth of the embryo *in situ*, was already established in the earliest phases of the transmigration.

Greater difficulties are met with in attempting to account for the present condition of the sporophyte; and it is these which have allowed the remarkable theory of the 'Origin of a Sporogonium by Progressive Sterilization' to receive a grudging acceptance; without any attempt to solve the question as to why such progressive sterilization should be either useful or necessary as a matter of life-and-death to the race. The purely idealistic nature of the conception is everywhere apparent; again, as a relic of the academic Pre-Darwinian outlook on nature generally, still so freely expressed in classification of Angiosperms, in grouping of 'natural' families, or in Brefeldian views of the phylogeny of Fungi. A pretty theory need not be accepted nowadays merely because it is plausible on paper, and is built to explain drawings rather than living plant-organization. Once the radial leafy shoot of the Moss-gametophyte is accepted as primitive, because it is nearest the normal organization of marine vegetation, it follows that the sporogonium must be of essentially the same organization, however much it may appear entirely different at first sight. For example, if 'leaves' are absolutely wanting on any living representative, it is clear that they must have been lost at some early period. The point is, when? Was it antecedent, or at a date subsequent, to the actual Transmigration? The analogy of the Florideae, in which a similar post-sexual and normally diploid phase deteriorates rapidly owing to parasitic nutrition, suggests the possibility of the former; the insistence of the water-problem to the dependent generation inclines to the latter. The case of the Florideae, again, is not strictly comparable, since the apparent resemblance of a cystocarpic ramulus to a sporogonium of a Hepatic, for example, is due to the suggestion of the cystocarpic 'wall' derived from the parental gametophyte; the carposporophyte itself is a purely deteriorated filamentous system of sporangial ramuli, even in its most complete expression (*Helminthora*). On the other hand, loss of foliage-leaves follows naturally in higher plants as the necessary outcome of intense insolation and desiccation, giving the 'cladode'-habit (cf. *Cactaceae*); and the Moss-sporogonium may be so far looked on as a 'cladode-system', in which photosynthetic laminae have been lost subsequent to the emergence of the algal form to more intensely illuminated subaerial levels. From another point of view, the deterioration of a *Riccia* may be compared with that of *Lemna*. That the sporophyte, even in its transmigrant habit, is still a wholly independent algal organism is shown most clearly by the very obvious junction, rather than a cytoplasmic fusion of tissues, and by the vestigial and apparently entirely useless 'rhizoids',

[1] The infinite variety and complexity of shoot-construction among marine algae appears to be wholly ignored by those, who in a serious discussion of the origin of Pteridophyta, would include reference to *Coleochaete*, *Oedogonium*, and *Sphaeroplea* (Tansley, loc. cit., p. 32). To those who cannot appreciate British sea-weeds, a glance through the plates of Harvey's 'Phycologia Australica' (1858) might prove suggestive, as a sample of the beautiful growth-forms of the sea, the organization of which requires detailed analysis.

[2] Guignard (1889), Revue Gen.: Belajeff (1894), Flora 79, p. 1.

retained at the base of the 'primitive' sporogonium of *Anthoceros*. Other arguments are perhaps even more convincing. The apophysis of higher Mosses, as also in a wholly distinct phylum as *Anthoceros*, shows an advanced condition of photosynthetic mechanism expressed in the complete equipment of a 'Transpiration-system'; involving (1) intercellular spaces, (2) aqueous epidermis, (3) cuticle, (4) possibly aqueous hypoderm, (5) suggestions of a distinct palisade-'mesophyll', and (6) normal functional stomata. In all higher Land-Flora (Pteridophyta, Phanerogamia) these factors are the undoubted equipment of the photosynthetic leaf-lamina, as exposed to bright light; and the presence of similar factors in stem-structures is usually accepted as the reflection of the organization of the 'leaf'. To account for the presence of such factors in the capsule of *Anthoceros* or *Funaria*, for example, it is necessary to suppose that these biological factors can be evolved wholly independently in exactly the same details in several wholly distinct transmigrant phyla of any horizon; or else that they are the equipment of a definite *leaf-ramulus*, at one horizon, once for all, which may be left behind on an axis with the suppression of the lamina-extensions. On the whole, the latter seems the line of least resistance; and it may be provisionally conceded that the prototype of the sporophytes of Bryophyta possessed radial axes, basal rhizoids, and distal leaf-laminae, as it still retains a segmenting apical cell, so generally associated with the same factors in marine algae.[1] Thus it may be noted that the peristome-less capsule of *Sphagnum* cannot be regarded as a degree more 'primitive' than that of the Bryaceae; since it possesses non-functional stomata, which are clearly vestigial rather than incipient. Hypotheses of 'sterilization', again, skate very lightly over such difficult problems as the evolution of a segmenting apical-cell: this again is a factor intelligibly acquired in marine phytobenthon; it is extremely difficult to connect it with any demands of the growth of a '*de novo*' post-sexual phase, as a matter of life and death to the organism.

Sterilization hypotheses are admittedly concerned more with archesporial tissue than with somatic organization; but all algal analogies again suggest that the 'immersed' archesporium is to be taken as the primitive case, as a single layer of potential *tetrasporangia*; a tetrad is identically

[1] 'Sterilization Hypotheses' curiously ignore such fundamental features as (1) the evolution of apical growth, (2) the evolution of the mechanism of an apical cell segmenting by oblique planes in three dimensions; such features being apparently supposed to come 'by nature'; i.e., to be 'reflected' into a new generation from the preceding: a peculiarly vague way of looking at things, considering other features which are not so reflected. As a matter of fact, these attributes are a part of the equipment of marine algae, and have been undoubtedly evolved in the sea as a response to the special problems of marine phytobenthon; and, so far as massive parenchymatous growth-forms are concerned, are correlated with a system of ramification in the shoot-system, to the extent that such a segmenting apical cell must be regarded as a mechanism to subserve the sequence and orientation of the laterals, rather than merely the spacing of the units of the tissues of a single axis. This applies with greater emphasis to cases of oblique septation, even in filamentous types of the Florideae, in which transverse septa are utilized to increase the axial series; but an oblique septum, thus involving the mechanism of a 'tipping' nucleus, characterizes the initial of a lateral branch; cf. *Polysiphonia fastigiata*, *Bonnemaisonia*, *Laurencia*, *Batrachospermum* from its *Chantransia*, and further afield in *Stypocaulon*. As no mon-axial plant of the sea carries such a segmenting apical, the presence of such an apical construction in the Moss-sporogonium may be taken as indirect evidence that the sporophyte-generation of the Bryophyta has wholly lost its capacity for ramification, if only in the form of the simplest ultimate ramuli as 'leaf'-members.

the characteristic limiting term of the benthic unilocular sporangium, in which meiotic mechanism determines the number four; and it is difficult to construct any other view to account for the origin and remarkable permanence of such a construction throughout all stages of higher Land-Flora. An 'immersion' of one covering-layer of surface-cells,[1] following directly the method traced in the evolution of the antheridium, would suffice; giving a differentiation of a central conducting region ('columella'), an archesporial zone, and a peripheral protective layer (epidermis or 'amphithecium'). Such differentiation may be traced, as a matter of fact, in the 'stichidia' of *Dasya* among the Florideae, on a small scale; but the physiological factors are there. A deeper immersion following subdivision of the 'wall'-units (amphithecium) in more massive sporogonia, as also a more highly emphasized storage 'columella'-region, do not add any essentials to the scheme (*Funaria*, *Polytrichum*); and all phases of decadence may follow, as by the reduction and elimination of the columella to the ultimate deteriorated version of *Riccia*. The conventional text-book series, as a series, is as easily read one way as the other. Details of dehiscence (Peristome, Calyptra), supply of the spore-primordia with water-storage (elaters), dispersal of the dried spores by wind, and the mechanism of the intercalation of a *resting-spore* at the close of the diploid phase, are obviously so much novel and secondary equipment of the land, and may be deleted from the organization. On the other hand these very factors, as representing the more recently acquired equipment of the subaerial phase, constitute indications of the lines along which modern divergence of genera and families has taken place, and may therefore be legitimately employed in the 'classification' of members of the group. The more fundamental distinctions of the larger groups may have their roots deep down in the benthic phase, and dorsiventral Hepaticae, for example, may have been dorsiventral from their first emergence, or even before; just as many dorsiventral Florideae may still retain a radially organized carposporophyte. While the tetrads with included meiotic division only repeat the mechanism of marine two-phase Florideae and Dictyotaceae; the increased output of these spores, and the greater concentration of the archesporial tissue, is to be regarded as the measure of the wastage of the new mode of life. In all early forms of Land-Flora, in which sexual wastage is reduced as far as possible by fertilization *in situ*, the great strain of wastage is felt in the phase of the air-borne spore which closes the life of the sporophyte individual. As in the case of phyla of subaerial Fungi, successful transmigration was apparently possible only to algae which had already acquired a two-phase type of Life-cycle, in which the sexual generation either had established, or was on the point of attaining, the ultimate phase of oogamic fertilization *in situ*, as leading to

[1] It is now possible to get an idea as to the phyletic significance of this superficial layer of the plant. In the marine phase the surface-layer of the organism, being the only layer in direct contact with the medium, is absorptive, adsorptive, photosynthetic, proteid-synthetic, and hence normally merismatic also. With the loss of the external food-solution, these functions largely vanish; in the gametophyte of land-flora, once removed from permanent submersion, most of these functions go at once; and the layer remains as merely 'protective'. Only in the sporophyte-generation does it add new transmigrant adaptations. The 'epidermis' of a land-plant, as it is henceforward termed, is so far *vestigial*, and devoted to new functions; becoming ultimately highly specialized in correlation with subaerial existence; with great 'protective' capacity of secondary value, but with little power of continued growth, and commonly non-photosynthetic. Only in the root does the older absorptive and adsorptive function have free play; and here it is the photosynthetic and proteid-synthetic functions which are necessarily obliterated in the dark recesses of the soil

consequent germination *in situ*, and the parasitism of the continuing diploid sporophyte; the latter in virtue of its asexual spores completing the 'alternation'. The fact that all higher land-plants present this scheme of '*alternation of generations*' was the essential discovery of Hofmeister, and has undoubtedly afforded a sure foundation for all later interpretations of the morphology of the higher plant-races of the land; though an academic conception of alternation, apparently for the mere sake of alternation, or equally fanciful ideas as to the virtue of haploid and diploid phases, may have led to confused lines of thought. Taking Land-Flora alone, as an isolated section of the vegetable kingdom, such alternation is presented, as a fact of observation there is no gainsaying; though any definite reason for it remains wholly unintelligible; as already noted, the speculations which culminate in the 'Origin of a Land Flora' of Bower (1908) sufficiently indicate the impossibility of getting further behind the scenes, so long as land-plants are alone considered. It now becomes apparent that such an alternation was a necessary factor in successful transmigration; no race without such an alternation has been able to pass from the sea to the land; and the situation is so far greatly cleared. The analogy of several phyla of two-phase Fungi affords the clue to the progression of the more successful autotrophic Moss.

With the continued necessity for an agency of *dispersal*, now expressed in terms of the moving medium of the atmosphere, and now eliminated from the sexual mechanism by the adoption of fertilization *in situ*, with consequent growth of the zygote *in situ*, the spores of the parasitic sporophyte similarly require to be shed in drier air. They hence not only assume the responsibility of the *perennation*-phase, but require to be provided with a mechanism of sporangial dehiscence and discharge. The factors in the organization of the reproductive tract of the sporophyte-generation are thus to be analysed under two headings:—

(1) *Primary factors*, as representing the retention of tetrad sporangial units, producing spores with perennation-mechanism of endospore and cuticularized exospore, capable of enduring a considerable degree of desiccation, and established as units of a definite volume ranging to 100 μ diam., as compared with the average 10 μ basidiospores of Fungus-phyla.

Cf. *Polytrichum*, 10 μ: *Marchantia*, 12 μ: *Sphagnum*, 12 μ: *Funaria*, 15 μ: the general range for Moss-types being low; though the more aberrant genera may rise to spores which compare very fairly in volume with the standard tetraspores of *Dictyota* (50–75 μ), or the range of tetraspores in higher Florideae; e.g., *Anthoceros*, 30–50 μ; *Pellia*, 80 μ, oval and septated; *Riccia*, 75–90 μ.

(2) *Secondary Factors* of sporogonial dehiscence and discharge, included as mechanism of annulus and operculum, peristome and elaters; cleistocarpic types presenting obvious stages of deterioration. Such accessory factors, as the newly acquired equipment of subaerial conditions, hence become the legitimate units of classification, delimiting the progressive new phyla as these seek their individual solutions of the new problems of the land. Since, again, the output of such air-borne spores now expresses the main wastage factor of the race, the economical regulation of the discharge becomes the most insistent of the new problems of reproduction; the greatest degree of variation in details of such mechanism is to be expected, and one arrives at last at the essential significance of the *peristome* in the most successful modern races of mosses as Bryineae: quite apart from the sub-conscious utilization of such factors by systematists of the Moss-series (because there was little else to classify by).

Subtracting these factors of the new subaerial equipment from the Moss-capsule, for example, the construction reduces to a few very simple

terms; no more than may be illustrated in many sporophores of the Florideae. The Bryophyte-sporogonium in its decadence similarly reduces to a monaxial capsule, of stalk, wall, contents, and dehiscence-mechanism, no more elaborated morphologically than a unit-ramulus which specializes as an antheridium; and such a reduction-scheme is readily intelligible; just as a reduced monaxial Cycad may be compared with one spur-shoot of an arboreal Conifer. The germination of the spore to a filamentous '*protonema*' may recapitulate the obvious 'juvenile stage' of many marine algae; while a simple abbreviation of such an embryo may be traced in the first divisions of the oospore within the archegonium (*Funaria*). Only in the last phases of decadence (*Riccia*), does the zygote segment in a more telescoped and mechanical 'octant'-phase, that recalls the 'breaking down' type of segmentation in the spores and zygotes of so many algae (*Fucus*, *Polyides*), and is undoubtedly equally secondary.

Though so far altered from its original condition, as to be almost unrecognizable as a type of massive phytobenthon, sufficient remains to show that the marine prototypes of the Bryophyta were:—

(1) Multiseptate (parenchymatous) algae, with radially symmetrical axis, leaf-ramuli, three-sided apical cells dominating the entire organization of the shoot, and rhizoid hapteron-system. Reproductive organs were borne on specialized lateral ramuli (axillary), in a condition of advanced heterogamy, to a degree approximating that of *Dictyota*; a diploid phase of similar somatic organization, possibly even free up to the time of the transmigration, bearing superficial sori of tetrasporangia; the spores on germination retaining a juvenile filamentous stage.

(2) At the transmigration, fertilization *in situ* is established (much as in *Chara*) with all the consequences of a parasitic diploid zygote. All reproductive ramuli acquire a superficial investment of a peripheral layer of cells (as 'wall'). Superficial sori of tetrasporangia become confluent to an archesporial layer, as wastage gives an increased demand. The diploid phase deteriorates by losing its leaf-laminae, apparently subsequent to a period in which they had been highly organized on normal 'leaf'-lines with stomatal mechanism. Features connected with the wind-dispersal of the spores are added; increased output compensates new wastage; and in the great majority of cases enfeebled gametophytes, restricted to the shade of other more successful transmigrants, reduce to dorsiventral shoot-systems, implying still further deteriorated, since ill-nourished and parasitic, sporogonia. In the limit, the latter become mere spore-capsules, deceptively 'primitive' by the loss of factors; the more so as the parent gametophyte is the more reduced by starved aquatic habit in fresh water (*Riccia*).

There is no need to labour the details of a mere sketch; it is sufficient to point out that the present story is at least as intelligent as the stock account of the sterilization of a post-sexual phase for no particular reason; *while it does present a view of the desperate struggles of transmigrant algal vegetation with insistent water-problems, and fatally handicapped by lack of any possibility of acquiring an absorption-mechanism sufficiently capable of dealing with the supply of necessary food-salts* (*nitrogen-problem*).

Perhaps the weakest point of the story that can be suggested so far is,— Why should the diploid sporophyte initiate a transpiration current, and its associated stomatal mechanism, when the homologous gametophyte, which started on equal terms, failed to do so? A little consideration, however, suggests that such a current was never initiated directly for the purpose of absorbing *water*; that any elementary organism can recognize the nature of its physiological problems and solve them directly is too much to expect.

The successful solution of any problem, as in the case of all biological mechanism, is always of the nature of an *adaptation* of something pre-existing. The transpiration-current, in other words, traces its origin to the haustorial absorption of *food* rather than water; the latter is not immediately insistent in a saturated atmosphere, though the necessity for food-salts may work out later; food-supply direct from the gametophyte is the first need of a parasitic zygote; and in so inducing a haustorial drain, an upward current may be initiated which may continue to take water. The gametophyte, with no such educational stimulus, never improved on the rhizoidal mechanism of marine algae; and hence remains permanently at the level of algal benthon, taking what salts it can by absorption at the entire surface of the shoot-system, in the primitive manner; so far starving on it where there is no change of the fluid medium and in damp air. In this way the nutrition of the diploid zygote *in situ* gives the impulse that was needed to initiate a transpiring subaerial organism in a sub-saturated atmosphere. That is to say, the transpiration-current which marks the essentially new physiological mechanism allowing existence in less and less saturated air, was never 'invented' *de novo* for its special purpose; it began as a mechanism of parasitic nutrition, and has been adapted to its special purpose; and, though in Mosses it has been correlated with a stomatal mechanism for the discharge of excess water, it has never achieved the ultimate stage of taking water directly from the external supply in the soil. In this way the weakest point of the story, at first sight, becomes one of the most remarkable confirmatory features; again opening up views of the problems of marine vegetation left with no supply of water or food-salts. Only comparison of the still more successful, as more dominant, Pteridophyta can demonstrate the point at which the Bryophyta have failed to go further ahead. Regarded as decadent and vestigial survivors of transmigrant algae, now highly specialized in a few minor lines adapted for inferior stations, the latter acquire an interest far beyond that conventionally attributed to them for the sake of their 'alternation of generations'.

The last standpoint of the indirect origin of the transpiration-current is the more interesting since it undoubtedly affords a clue to a wider outlook, as:—

(1) The transmigrant algae which gave rise to the characteristic subaerial sporophytic stages of both Bryophyta and Pteridophyta had necessarily attained to the limiting reproductive phase of 'fertilization *in situ*' at the time of the transmigration, or attained to it in the process of transition: since the diploid phase had had little time to deteriorate.

(2) The fact that no alga, however distinctly it may be demanding water to compensate desiccation of the exposed shoot-system, can necessarily initiate a conduction-system to supply the loss, directly, by mere osmotic absorption at the wet end, or can be visualized as understanding what is the matter; though taking synthesized food-material may be a subject within its range.

(3) Confirmation of such deductions is afforded by the general case of all Fucaceae exposed on the littoral tide-range, or in muddy estuaries, to which further transmigration remains barred by the fact that they do not show any tendency to initiate any such upward current; while the lack of fertilization *in situ* is now seen to be the determining factor which has held them back from the land; as also the lack of a diploid phase germinating *in situ* has debarred the *Characeae*.

(4) The transmigrant algae were distinctly not members of the Fucaceae (*Cystoseira, Sargassum* series), although they may have combined in many respects the parallel evolution of massive stem and leaf-ramuli, as also the three-sided apical cell, so clearly expressed in these types; but they were undoubtedly of the highest order of marine benthic types, both somatically and in reproductive equipment, that the sea is capable of producing; and by no means mere effete relics of green transmigrant algae of fresh-water ponds (!).

Note on Stomata: The mechanism of the evolution of a stoma remains wholly obscure. Intercellular-spaces trace their origin to the drying up of all intercellular mucilages, or their restricted production in growing tissues, as well shown in the changes in fucin-derivatives of the mesochiton region in Phaeophyceae, as *Ascophyllum* and the permanently submerged *Halidrys*, in the construction of pneumatocysts utilized for erection of the thallus: Cuticle is only the chemical specialization of stratified lamella of polysaccharide of the outer wall (exochiton): Palisade-cells may be differentiated as in *Himanthalia*; a colourless peripheral layer is elegantly marked in the Floridean *Scinaia*; but the opening up of chinks between cells communicating with the exterior, and the ultimate control of such chinks by sister guard-cells, involves a series of events difficult to trace, of solely subaerial nature, and with no direct foreshadowing in the sea.

It may be pointed out that:—

(1) The slit between the two guard-cells is of the nature of an intercellular space continued in the peripheral layer.

(2) The intercellular spaces were certainly not formed for the aeration of massive tissue, since the atmospheric oxygen-supply was far beyond anything to which the tissues had been accustomed in the sea.

(3) Nor were they opened up for supply of CO_2, which passes as readily across a wet membrane as across air.

(4) But apparently for the discharge of water as vapour or fluid, owing to the new and completely altered conditions of the supply of food-salts (nitrogen-problem).

(5) The photosynthetic cells of the organism, previously in direct contact with the food-solution of the sea, and adsorbing ions from it directly as required, are now restricted to what they can get from the general surface-absorption of rain-water, or from the mechanism of a transpiration current.

(6) In the last case a great volume of water has to be taken with the salts it may contain, and the excess discharged to the exterior; a state of affairs which constitutes perhaps the most remarkable change of nutritive mechanism ever effected in terrestrial organism, and more completely delimiting the land-*plant* from the land-*animal*.

Summary. (Bryophyta.)

(1) Given a two-phase cycle of autotrophic algal category, the general facts of the progression through the transmigration epoch were *inevitable*; since provision for the dispersal of air-borne spores could be only normally intercalated in the spore-stage of the parasitic asexual generation.

(2) The immobile air-borne spores of land-flora are thus the lineal descendants of the tetraspores of an advanced algal unilocular sporangium, now immersed in the somatic tissues.

(3) Beyond the evolution of the endogenous air-borne spore, in which the Bryophyta closely parallel the progression of Higher Fungi, a special departure is noted in the origin of the *Transpiration-current* and its associated *Stomatal-mechanism*, also restricted to the parasitic sporophyte-generation, which so far surpasses the gametophyte in new anatomical and physiological equipment, as it does in the newly acquired mechanism of the immersion, nutrition, and discharge of the air-borne spores.

(4) In this way the sporophyte-generation acquires new factors of organization far beyond those of the aquatic gametophyte; though still feeble in point of relative size since further progression is barred by the lack of auto-absorption of salts from the food-solution of the soil; the asexual phase thus dwindles as it presents further starvation-effects, as a parasite on a starved aquatic of rain-water solutions.

(5) Hence Bryophyta remain as vestigial relics to point the moral a

failures on the whole in transmigration, as compared with more successful Pteridophyta; though in many points of autotrophism superior to the heterotrophic Fungi. They thus remain restricted to the most inferior biological stations, demanding no depth of soil, but a more or less saturated atmosphere.

XI

PTERIDOPHYTA

In many respects the phyla included as Pteridophyta follow the general trend of progression observed in Bryophyta, with a degree of parallelism which marks, in fact, the most significant feature of their evolution, as it was the earliest to be interpreted (Hofmeister); as indicating again not so much an actual basis of affinity, as a community of experience, and adaptation at a similar horizon to the same conditions of environment. The same sequence involving a subaerial sporophyte-generation obtains, the latter producing tetrads of air-borne spores, and following the fertilization *in situ* of a definite archegonium-mechanism, comprising 'neck', 'neck-canal cell', and 'ventral canal cell'. The general scheme of the transmigrant organism is again clearly defined; the tetrads being known to include meiotic phenomena as the lineal descendants of marine tetrasporangia; while advanced oogamy is again correlated with the retention of a flagellated zoïd, though of a type so distinct from that of any Bryophyte (so far as Filicineae are concerned), that it can be only accepted as evidence of a wholly distinct race of presumably 'green' algae, dating back independently to the Flagellate phase of the sea.

Although the mechanism of successful transmigration may be closely similar, agreeing with the general deduction that there was only one way to the land, and that all successful transmigrant vegetation has come the same way; the phyla of the Pteridophyta clearly differ widely in many fundamental respects from the transmigrant survivors of the Bryophyta. Thus it is so far evident that:—

(1) Transmigration to be effective can only take place in an algal phylum which had attained fertilization *in situ*, and in which a diploid phase has proceeded to tetrad asexual spores; since the former alone gives the attached zygote from which springs the possibility of a new phase of somatic organization (with basal absorptive mechanism); while the latter can alone produce the tetrads of air-dry spores adapted to the new conditions of subaerial dispersal.

(2) But beyond the condition of the modern Bryophyta the Pteridophyta are equipped for a further advance, in that the possession of massive *crampon*[1] hapteron-systems gives them the power of independent 'rooting'

[1] By *crampons* are indicated the massive ramuli utilized as secondary hapteron-system in many marine algae, arising polyphyletically in many distinct phyla (*Durvillaea, Macrocystis, Turbinaria, Phyllospora, Dictyota radicans*, of the Phaeophyceae; and among the Florideae in such forms as *Callophyllis, Furcellaria*, and *Thamnoclonium*; perhaps most conspicuous and familiar in indigenous Laminarians. A distinctive and characteristic name is wanted for these remarkable organs, once they are recognized as the forerunners of the roots of higher plants. Even in the bilateral *Laminaria*, these structures are already vestigial, arising as centric ramuli, retaining the dichotomous ramification of an older horizon; but utilized and

in the sporophyte generation, and the consequent attainment of an individual connexion with the land-surface of 'soil'; which by initiating the root-system with successful internal water-current, marks the true commencement of the domination of the new conditions of 'land'-vegetation; the evolution of 'soil' being in all probability simultaneous with the evolution of the 'soil' inhabiting plant.[1]

The tentative haustorial current of the Bryophyte-sporogonium is thus superseded by the full mechanism of an efficient transpiration-system; proteid-synthesis of the green parts is provided for by a new source of salts; and again in apparently the only way possible. A readjustment of the entire anabolic machinery is thus effected; the superficial photosynthetic tissues being now supplied with food-salts from behind, as it were, instead of from the surface exposed to the outer medium. This is undoubtedly the most striking rearrangement of the internal economy of the plant that has ever taken place; a difficult and wholly unforeseen solution of the problem;

adapted for a secondary function of attachment. Morphologically they express the first condition of the somatic ramification of more massive growth-forms, of the level of the more elementary type of *Mesogloia*; but now relegated to the basal part of the plant, and hence presenting a growth-correlation with the main axis which involves a basal direction in growth, in the manner foreshadowed by what are commonly known as descending rhizoid-filaments of a filamentous soma. The morphological origin of the 'root' presents a vista of distant marine origin, as ancient as that of the 'leaf', from the first somatic ramuli of massive phytobenthon.

[1] The physiological introduction of *positive geotropism*, so commonly regarded as an essential feature of a 'root', is again wholly secondary, and of subaerial origin. There is no sign of geotropic response in the sea: a moving medium affords no opportunity for stopping to acquire a delicate perception of the weight of one's cytoplasm. The one insistent stimulus is that of light, and positive heliotropism is the primary expression of irritability in the plant-kingdom. Much confusion of thought exists with regard to geotropic response as a causal factor in the relations of 'stem' and 'root'. It is important to note that geotropism only comes into operation in subaerial stationary organism, and the mechanism of irritability originally elaborated to effect a response to light, may be utilized to respond to some other physical agent, just as *Mimosa* responds to contact, &c. Geotropism thus appears as an adaptation. Its origin is definitely polyphyletic, since its utilization in subaerial fungi can have no connexion with the same response among Bryophyta and Pteridophyta. Among Fungi, as Buller has shown (1909, p. 65), both positive and negative response occurs in different regions of *Agaricus*; while *Polyporus* may present positive, negative, and diageotropism: the response to gravity being clearly not so much causal, as the refinement of a preceding growth-mechanism, utilized to give increased precision of orientation with the vertical, in these cases with a view to spore-dispersal.

Similarly in the case of the positively geotropic root, and the negatively geotropic stem of land-plants, the stem had already a mechanism of positive heliotropism before emerging from the sea. Negative geotropism only assists and makes more precise a previous sense, and gives increased accuracy of vertical orientation when mechanical aids to support are required in the stem-tissues. In the case of the crampon, with antecedent structural bias in favour of descending growth, a positive response is in turn utilized to increase the accuracy of vertical descent, more particularly as such organs work in reduced light. In total darkness, as in soil, such geotropic response remains as the essential guiding factor. In spite of all futile academic disquisitions on the theory of 'shoot' and 'root', the primary root of the Phanerogamic embryo is but a precocious crampon; the terminal position of which is secondary, and hence wholly unintelligible to the morphologists of the land-plant. No physiological or morphological problem of subaerial vegetation can be satisfactorily outlined, which does not take into consideration the early beginnings of all such phenomena in the sea.

however natural it may now appear to us who study land-types first, and conceive a plant as evolved to run as a subaerial mechanism only In this way the transpiring vegetation of the land becomes more and more marked off from lower 'non-vascular' types.

As successful solutions of the problems of transmigration become the more pronounced, so the connexion with antecedent algal phases becomes the more obscure, since overlaid by new departures. The more fundamental features of the older scheme may be examined from the standpoint of:—(1) the organization of the leafy-sporophyte; (2) the mechanism of absorption and nutrition; (3) the nature of the reproductive organs (sporangia); (4) the reduced relics of the sexual processes.

I. Taking the generalized conception of the Fern-type, as that of a plant with radial organization in its main axis, and bearing lateral frond-systems, as multibranched bilateral constructions, ramifying with pinnules to the 2–3–4th degree, and borne acropetally in Fibonacci order on a comparatively feeble (since non-ramified) axis, the growth of which is controlled by a 3-sided apical cell,—there is no difficulty in homologizing such a somatic form with the generalized type of thallus characteristic of many of the larger Brown Seaweeds, as in the *Cystoseira*, *Cystophyllum*, and *Sargassum*-series; among which a great range of type still exists to demonstrate the possible variations on such a theme, even in the sea. And other factors are agreeable: e. g:—Trichome-derivatives, as rhizoid-hairs, still obtain as peripheral growths; the Fibonacci sequence of the leaf-ramuli bears no direct relation to the segmentation of the apical cell; the laterals as advanced bilateral systems present mosaic ramular arrangement, with the 3-sided apical replaced by its bilateral equivalent; massive crampon-growths, presumably also with 3-sided apicals, foreshadow the adventitious root-system of the Fern (*Cystophyllum*, *Sargassum* (sp.), *Turbinaria*); the space-form factors of the frond-system are so curiously parallel, that whether dichotomous 'venation' be regarded as the older expression of dichotomous 'ramification' or the converse, the types of the *Sargassum*-series include all variants. The Fern only differs in the final specialization of dorsiventrality in these main lateral frondose ramuli, as the latter acquire a more fixed light position; even circinnate vernation is a phenomenon of the sea in several distinct phyla. It is impossible to doubt that the *form-factors* of such frond-systems are all to be traced primarily to marine phytobenthon, and in more than one phylum. The fern-like characters of the fronds of many Florideae have been a continual source of admiration to generations of algologists; even in *Halopteris filicina*, of the isolated Sphacelarian type, the 'imitation' of a fern-frond may be expressed in actual numbers and proportions of pinnules to the 4th degree, closely identical with the laminae of *Aspidium*; all the ramifications being worked out in terms of a simple filamentous soma with an 'apical cell' for every ramulus. While the production of such frond-systems may be *homoplastic* for marine environment, in Sphacelarian, Fucoid, and Floridean, it is more than straining a point to conceive the independent evolution of such organization, in so closely identical a fashion, in an environment of wholly different exposed subaerial conditions. The balance of evidence inclines to the view that such form-factors must persist in the race, as part of the inherited equipment of the sea; they may be varied, adapted, deteriorated, superseded, in infinite range and detail, but not *recreated* wholly anew by land-vegetation. The theoretical derivation of a land-'leaf' from an algal lateral ramular system is as insistent as that of the land-'root' from the algal crampon, as a residual type of indefinite and uncontrolled ramification of the oldest benthic axes. In fact, if no confusion had been introduced by the complexity of the sexual cycle, the somatic

organization of a Pteridophyte, so far as the sporophyte-generation is concerned, might have been traced back to the sea, as obviously as can the construction-factors of the soma of land-Vertebrates.

II. In internal (anatomical) organization the differentiation of tissues, again, follows the lines laid down in Bryophyte sporogonia: *intercellular spaces* are opened up; and these communicate with the exterior by *stomata*, similar in details of mechanism; *cuticle* is secreted over the exterior, and a distinct *epidermis* is localized to clothe all parts in contact with sub-saturated air, giving the control of a single layer of living cells to all the organs of the plant except the absorbent crampon roots. The *vascular system* is initiated, for the first time, in terms of a definite ascending current, replacing the 'descending drift' of the sea-weed, which remains in *phloem*; and *xylem* is constituted essentially of *dead* cell-units, now utilized for the first time for conducting purposes. That is to say, the first cells to die from the effects of insistent water-problems are the 'storage and skeletal' internal units of the axis, as these are drawn on by the superficial photosynthetic tissues; and the first dying cells become the first tracheides; the latter again acquiring a thickening of the wall, whether as special adaptation to prevent collapsing under pressure, or primarily the expression of accumulated polysaccharide waste in moribund protoplasts. In a centric axis such a strand is centric; in bilateral ramuli it is also bilateral; and by the connexion and junction of such strands (xylem) is ultimately built the 'dictyostele' of the main axis; when the latter is small and without any necessity for a supply of its own. The main fronds of the Fern-type are still the special glory of the race; and they so far undoubtedly represent the retention of the frond-systems correlated with a reduced main axis familiar in many marine types (*Cystoseira*, *Sargassum*). It may be pointed out that ontogenetic recapitulation of such structural factors is not necessarily reliable, and may be much over-rated; just as it is in vain to look in mammalian embryology for the determining factor which led to the metameric segmentation of vertebrae. The ontogeny of the first exogenous crampon-root of the Fern-embryo may again be more significant than the endogenous production of ultimate root-systems; just as the crampons of old stems of *Laminaria Cloustoni* are distinctly 'endogenous'.

With the attainment of the independent habit of a land-plant, the question of the mechanism of nutrition under subaerial conditions becomes acute; and owing to the fact that problems of subaerial nutrition have been always given first place in Land Botany, it is not generally grasped how aberrant such methods appear when viewed from the standpoint of the advancing vegetation of the sea, or in what the difficulties of the new problems consist. It is not too much to say that the problem of nutrition might well appear at first sight wholly insuperable; and the fact that plant-life has survived this epoch to successfully dominate the land, is perhaps the most wonderful aspect of all higher vegetation. Since an apparently indefinitely complex mechanism has to be wholly readjusted, while still running, in a manner it was impossible to foresee. Incidentally it may be noted that this is always the peculiarity of advancing organism.

The case of the Bryophyta presents comparatively little difficulty; the sporophyte being still entirely dependent on the parent gametophyte for water and food-salts. The fact that it may open up intercellular spaces, continued to the external surface as stomatal mechanism, apparently following the effect of excess photosynthetic oxygen, as in the case of marine algae (pneumatocysts), has little bearing on the question of food-salt supply; except in so far as it may be interesting in throwing light on the fact that stomatal mechanism may precede an efficient transpiration current in phylogenetic origin.

But in the Pteridophyta the novelty of the subaerial conditions may be more fully analysed. Emergence from the water increases the amount of available oxygen illimitably; to pass from a medium with about $\frac{1}{2}\%$ of the free gas to one

with a content of 20%, may be said to solve any oxygen-problem that can normally arise: no necessity for storing photosynthetic oxygen for katabolism during the night-period need henceforth be considered: 'respiratory-pigments' are of little significance, and may be scrapped: chlorophyll, carotin, &c., appear solely as assimilatory pigments, or as accidentia which may take on a secondary biological utility, as in the colours of flowers. Carbonic acid-supply is, it is true, diminished; but owing to the gas being equally diffusible in water and air, the supply may remain satisfactory. Light-supply is considerably intensified owing to diminished absorption by the medium, as well as by the effect of a longer day. Even in this country, with the feeble insolation of the N. Temperate zone, according to Brown and Escombe (1905), the light-supply is far beyond the demands of indigenous vegetation as expressed in carbohydrate-synthesis.[1] On the other hand, the salt-supply has practically

[1] The photosynthetic mechanism of an autotrophic plant is admittedly sufficiently miraculous, but admiration for it need not be allowed to obscure the fact that mere accumulation of sugars or polysaccharide is of no use whatever to a plant as a growing organism, unless materials for further proteid-synthesis are at hand. Recognition of photosynthesis in the foliage-leaves of land-plants, dating from Sachs, 1862, has possibly led to neglect of the fact that the nutrition of the growing plant is still controlled by the absorption of solutions containing the necessary ions *via* the root; and that it is the dissociation of these two functions that constitutes the initial problem of the land-plant.

In an ideal plant-organization, photosynthesis of carbohydrate and proteid-synthesis should be accurately balanced, and accumulation of carbohydrate 'reserves' should never appear, any more than an animal should store fat. The evolution of the mechanism of storage is still illustrated in marine algae:—

I. Active photosynthesis during hours of insolation, by leading to excess carbohydrate production, enables the plant to continue to carry on proteid-synthesis during the night-period with the material on hand, so long as this may be readily diffusible or capable of being immediately hydrolyzed. Thus the Phaeophyceae, by accumulating carbohydrate in fluid physodes (*Fucus*), or as laminarin soluble in the cell-sap (*Laminaria*), acquire a most efficient mechanism, as a solution of the day and night problem; and the reserves may have other uses.

II. On a wider time-period, the same applies to the annual incidence of dark winter months, as in these latitudes, when photosynthesis practically ceases, with the limiting case of the arctic day and night. In such case excess storage of polysaccharide in a less readily diffusible form, e.g. as more solid granules, may result in dense accumulations of 'food-reserves' during the lighter months, which will enable the plant to continue to grow, and more especially to reproduce, during the months of darkness. Admirable examples of this idea are the commonplace of many common Florideae with dense accumulation of storage amylodes of readily hydrolyzable nature (*Polyides*, *Furcellaria*). In all cases of massive plant-organization, again, the problem arises sooner or later of the nutrition of parts to which neither light nor nutrient solutions can any longer penetrate. Hence the mechanism for the storage of polysaccharide food-material is initiated in the sea, as the response to problems of light-periodicity; as again other accumulations of excess polysaccharide material, not readily hydrolyzed at all by the plant, may find expression as wall-débris, which may acquire a mechanical or skeletal value, more particularly in the form of celluloses.

On transferring such a plant to subaerial environment, the intensified insolation of open air intensifies the photosynthetic 'reserves'; but the dissociation of the nitrogen and phosphorus problem tends to completely upset the balance of photosynthesis as leading to proteid-synthesis; and the land-plant becomes loaded with carbohydrate reserves without knowing exactly what to do with them. Storage of sugars, starches, and cellulose, become the characteristic of plants exposed to intense sunlight with little water-absorption; and the xerophytic plant is identified by its deposits of waste polysaccharide. The problem of how to get rid of the excess

vanished with the withdrawal of the medium; that is to say, photosynthetic operations are intensified, but proteid-synthesis requiring ions of Nitrogen, Phosphorus, Potassium, Calcium, Magnesium, &c., is at a standstill. Not only so, but the only available supply, other than the small amount available in rain-water, will be that carried up the axis of the plant from the substratum, and introduced to the photosynthetic units as it were from the rear. Instead of taking N and P ions only from the external medium as required, these substances are henceforward only available in very dilute solution in the transpiration current, so that a great volume of water has to be taken up as well. Thus taking the general nitrogen-content of the sea as about one part in ten million; for every gram of nitrogen, equivalent to about 6·37 of dry proteid (90 % water, or 63·7 g. of aqueous plasma, ten million grams (10,000 litres) of water would have to be pumped up through the plant, and secreted or evaporated at the surface; or at the rate of over 150 litres for one gram of plasma (without allowing for any selective absorption by the cells in contact with the source of supply). The labour may appear fantastic,[1] yet some such process is the only hope left open to subaerial vegetation; and, as we know, the chances have been taken. The transpiration-current, once set going, may be emended and perfected; as it will also bring other consequences in its train. While in the hypothetical case of a saturated atmosphere such a volume of water could be only got rid of by active secretion through primitive stomata as water-pores; a progressively sub-saturated atmosphere with attendant desiccation, now appears as a blessing in disguise, as affording the most welcome aid to the plant-cells, in mechanically assisting the removal of excess water, and so stimulating the flow of the current. *In fact proteid-synthesis, including growth of the organism, only becomes effective in the presence of efficient evaporation.* The transpiration-current thus solves the problem of food-salt supply, rather than the mere question of water-supply with which it is more usually associated in the case of xerophytic land-vegetation.

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and redress the balance is seen in the development of fruits and seeds, as also in the timber-tree. Human conceptions, based on horticultural and agricultural devices for increasing the yield of carbohydrate, do not necessarily run concurrently with the needs of ideal organism, any more than does the rearing of fat cattle. The ideal of converting the plant into a machine utilizing all available solar energy for the production of carbohydrate is agricultural, not biological.

[1] An admittedly extreme estimate, taking the value of combined N in sea-water as varying from 1–2 milligrams per litre (Raben). Accurate data for the amount of combined Nitrogen in soil are wanting, owing to the adsorptive effects of clay and humus; but suggestions from drainage-waters indicate the approximate value. Total Nitrogen as Nitrate (NO_3) and a trace of ammonia vary from—

(A.) 1 part per million, poor land, Germany; or 2·2 N in ten million.

(B.) 15 parts per million, Rothamsted field (Russell, 1915); or 3·4 part N per million.

(C.) 62 parts per million, manured field (ib. p. 66); or 14 parts N per million.

(D.) while a Laboratory 'food-solution' containing 1 g. KNO_3 per litre would be expressed as approximately 14 parts N in a hundred thousand.

These results may be roughly visualized as giving a solution to be absorbed as sufficient to build one gram of cytoplasm:—

A, 75 litres; B, 4 litres; C, 1 litre; D, $\frac{1}{10}$ litre.

Such a series, if only approximate, serves to indicate the insistence of the Nitrogen-problem in land-vegetation; and that plants preferably require decomposing material in the 'soil'; the probable cumulative effect of storing the precipitated combined Nitrogen of the atmosphere, and the advantage of mechanisms for fixing atmospheric Nitrogen as a last resource. Such considerations afford a further view of the increasing amount of polysaccharide-waste, as in more intense insolation the ancient balance between photosynthesis and proteid-synthesis is more and more disturbed; and the timber-tree fills up with dead skeletal débris of celluloses and associated compounds.

Not only so, but all plants that have solved the problem of food-salt supply must have solved it in the same way: a system of rapid water-absorption, conduction, and evaporation, in terms of older cell-equipment, will be polyphyletic in all transmigrant phyla. All must follow the same lines to be successful; and absorbing root, tracheidal vascular system, intercellular spaces and stomatal control, henceforward become the commonplace of all subaerial vegetation, *from whatever flagellated race or algal phylum they may have originally traced their origin.* These morphological and anatomical details are in turn no necessary guide to affinity; they are factors of the new biological equipment necessitated by the changed environment. Free-living autotrophic cryptogams are of necessity 'vascular', and may have originated not only from distinct algal series, but from benthic phyla following along on parallel lines of progression from even remote plankton races of flagellates.

III. Even more striking are the algal relations of the archesporium and spore-tetrads, unconvincingly traced as the outcome of long acts of 'sterilization'. Spore-tetrads with phenomena of meiosis, evidently controlling the number *four*, are familiar enough in the sea, in which a reason for the reduction to the minimum number of mitoses is apparent; and the spore-tetrads of a fern, in mechanism and origin, as well as in actual adult size, are no more than the tetrasporangia of the Florideae and Dictyotaceae, which have now acquired a completely 'immersed' position in the soma; so found in many of the more massive Florideae, in layers or sorus-patches (*Rhodymenia palmata*), beyond which the only new departure consists in the addition of the continuous protective epidermal layer (the special feature of the land-plant). The 'archesporium' thus appears in the general case '*hypodermal*', and has been so accepted by the generalization of subaerial botanists (Goebel).

The view of a continuous stratum of archesporial cells being normal for older fern-laminae, followed by the progression of sorus-restriction, and the localization of smaller patches to a system of more elevated outgrowths (*sporangia*), as secondary emendations for wind-dispersal, is but the continuation of the accepted evolution of the Eusporangiate and Leptosporangiate forms, included in the general account of the progression of Land-Flora (Bower, 1891).

With the attainment of a greater capacity for dealing with the conditions of sub-saturated air, however, comes the greater strain of the water-problem; and in the primary possibilities of the new environment the 'wastage-coefficient' rises enormously. With increase of wastage follows the necessity for increase in bulk of the plant. Megalophylly, photosynthetic efficiency and proteid-synthesis rise in corresponding degree; the aerial wastage being far greater than that of the spore-stage of the original benthic sea-weed. Thus a common fern of these latitudes (*Aspidium Filix-Mas*) may still show a wastage of 500–1,000 millions of spores per plant a year; the spores are of considerable size (30–50 μ), and such a coefficient of wastage works out at about 1,000 times that of the Laminarian (isogamous). The homosporous Pteridophyte still makes good this wastage; though in other phyla the progression of heterospory obtains with conspicuous results. The heterosporous Filicineae are the smallest, as well as the most feebly nourished, of their class, surviving only in the most inferior biological stations.

IV. While the coefficient of wastage in the case of the air-borne spores of the new environment is so enormous, demanding a vastly increased bulk in the organism (cf. Tree Fern as *Alsophila*, 60 ft. high); the gametophyte, having progressed through the full range of oogamy to fertilization *in situ*, shows sexual wastage well within the control of the sexual plant; it has been previously pointed out that this is immediately reflected in the extremely small size of the prothallus, its precocious reproduction and ephemeral existence. A matter of a few weeks only, in the case of *Aspidium*

(or ferns in general cultivation) sees the sexual plant replaced *in situ* by an organism larger than itself, much more capable of independent growth, and dominating the soil-conditions. While the somatic part of the prothallus is thus reduced to the lowest expression of a bilateral thallus of 'disc' habit, even more depauperated than that of *Anthoceros*, the relegation of the reproductive organs to the lower surface is correlated with the chances of the condensation of the smallest drops of water as the necessary external medium of the plankton-phase. The reproductive organs are further diminished in number and volume; though again less so in *Aspidium*, than in *Anthoceros* and Eusporangiate types, or in the still more reduced and ephemeral prothallia of Heterosporous Filicineae. Thus *Pilularia*, with non-autotrophic megaprothallus, produces a complete structure in 48 hours from germination (Campbell, 1895); and within a week the first green leaf of the sporophyte ('cotyledon') is established and recognizable. The consequent efficiency of the sexual mechanism in *Aspidium* may be rendered as obvious by comparison with such an advanced type as *Pilularia*, as by reference to the more massive and more numerous reproductive organs exposed at the ends of the leafy shoots of Musci (*Polytrichum*): for example; the development of the reproductive organs and embryo exhibit an annual periodicity (*Polytrichum*), spread over several months. In all cases it must be noted that the apparent morphological 'decadence' of the prothallus is associated with greatly increased biological efficiency in the reproductive mechanism; the aim being clearly the production of a new sexually produced individual in the shortest time, with the minimum of wastage; and not merely recapitulation of phylogenetic stages for the sake of the thing. Once the new embryonic sporophyte has attained independent attachment to the substratum, the responsibility of the gametophyte is at an end. *The minute size, and ephemeral existence of the latter, thus afford evidence of extreme efficiency, rather than of mere decadence; as, on the other hand, the increasing mass of the sporophyte generation equally implies biological inefficiency in combatting the rigours of the novel conditions of primitive subaerial exposure.* Mere size, as judged by our perceptions, being no criterion of success, and quick returns more significant in the improvement of the race.

Accepted text-book versions of the correlated increase in the volume of the land-sporophyte, and the deterioration of the old aquatic gametophyte, constituting the 'alternation' of generations of the Pteridophyta, are not merely the presentation of the rise of a new and dominant race, as the expression of the intensity of the wastage of subaerial environment following new opportunities of progression. The sexual process continues to become still more efficient as the sexual plants become non-autotrophic; and in the limit (Angiosperm) there is no sexual wastage (in the form of waste sexual nuclei) at all. When the problem of the dispersal of wind-borne spores can be satisfactorily solved, the sporophyte will again reduce in size, as it increases in efficiency and time-saving; giving as we know the case of the annual and ephemeral herbaceous plant with insect-pollinated flowers and 'quick returns',

Identical generalizations apply to the reduced prothallial stages of *Equisetum*, as compared with the sporophytic system; the discrepancy being still more obvious in earlier arboreal Calamites, in which spore-output and excessive wastage expresses the difficulty of the early assumption of the land-habit at great expense; though phases of progression to heterospory are known to have been established in a few types of the Palaeozoic. In other respects the diminutive character of the foliage-leaves, the tendency to symmetrical phyllotaxis-constructions, above all the dominance of the expression of intercalary growth-zones in the axis, and axillary bud-formations, may be quite possibly taken to suggest a derivation from some algal

phylum of the same generally flagellated ('multiciliate') class, but with divergent morphological organization of the shoot-system, even in the phase of submarine environment. That is to say, there is little reason to suppose that these peculiarities are *solely* the expression of adaptation to secondary subaerial existence, any more than a similar interpretation would be given to marine forms of *Sargassum* with dichotomizing filiform ramuli, to *Cystophyllum* with awl-like segments, or to the indigenous *Cystoseira ericoides* with three-sided apical cell and acicular leaf-ramuli in close spiral series.

In the case of the conventional series of the Lycopodineae, however, the condition of affairs is widely different in many features of fundamental significance; though a general parallelism may be still traced in special features of subaerial progression, and the phyla are so far convergent. Taking *Lycopodium* and *Selaginella* as forms alone fairly well-known in essential details, it is interesting to note:—

(1) The absence of the characteristic and dominant three-sided apical cell-mechanism; though bilateral cell-segmentation may be general in reduced bilateral shoot-systems of *Selaginella*.

(2) Prevailing dichotomy in shoot-ramification (i. e. after the manner of *Laminaria* rather than *Fucus*).

(3) While the prothallia are more or less specialized, with new biological departures of saprophytic habit (Lycopods), or heterospory (*Selaginella*), the flagellated antherozoids are small and characteristically *isokont*, of the simplest type; apparently even more so than those of *Chara* and the Bryophyta. Though the case of antherozoids, as also of spermatozoa which are motile within the body-cavity, and are never discharged into the open aqueous medium, may be open to objection from the standpoint of primitive factors of construction (cf. Cycads and *Gingko*), whereas in all *Pteridophyta* such flagellated zoïds are set free in rain-water or dew only, no adequate reason can be given for any secondary differentiation in primary details of flagellation; and the assumption is apparently legitimate, that such organization must date back to a flagellated plankton-epoch. It appears impossible to avoid the conclusion that the Lycopod phyla only merge with those of the Filicineae in a distant plankton-phase, even beyond an independent origin as benthic sea-weeds; and all subsequent progression in the two series is the expression of a parallelism of progression throughout subsequent phases of benthic to xerophytic conditions, rather than any indication of direct affinity.

For *Lycopodium clavatum* Bruchmann[1] (1898) figures a small zoïd with isokont flagella, two body-lengths. For *Selaginella cuspidata*, Belajeff (1885), a similar elongated zoïd with flagella twinned in the same direction, three body-lengths. The unavoidable deduction that the flagellate ancestry of the Lycopod series must have taken a wholly independent course through the algal phase of the sea, to complete the parallelism of progression on the land, is one of the most remarkable in modern Botany; and while it affords a clue to the *inevitable sequence* of the physiological progression of algal life right through the subaerial transmigration, it also affords a much needed explanation of the discrepancies observed between the great Lycopod and Filicine series, as:—

(1) The Fern phyla appear more generally associated with the advancing organization of the Gymnosperm series, as also confirmed by the retention of a multiciliated zoïd.

(2) The Lycopod alliance appears persistently microphyllous, as if without power to increase specialized leaf-laminae, though Palaeozoic Lepidostrobi compensated an enormous wastage output.[2]

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[1] Cf. Pritzel (1900) in 'Engler and Prantl', p. 592; Treub (1884), Ann. Jard. Buitenzorg, iv. p. 106, *L. Phlegmaria*.

[2] A particularly fine *Lepidostrobus* cone, described by Renault and Zeiller

(3) The rise of the Vascular system in the two series, being wholly independent, need not run absolutely concurrently; so that the Lycopod axis (*Sigillaria*) affords no necessary guide to the Conifer or Angiosperm stele.[1]

(Seward, 1910, 'Fossil-plants', p. 185) may have been 500 mm. long and 60 mm. diam. The tree probably bore many such gigantic strobili, though the same spore-output might have been put in more numerous smaller ones. But such a strobilus, if only containing 30 μ spores to half its volume, might have had an output of about 25,000 *millions*.

This may be compared with the microstrobilus of a modern *Araucaria brasiliensis* (Burlinghame, 1915) with an estimated output of ten million per staminate flower; the lineal descendant of a homosporous strobilus, showing so far a distinct gain on the part of the seed-plant.

A modern *Pinus*, probably the most efficient of modern Conifers, may easily produce a litre of pollen per tree, or something like 10,000 millions of microspores per annum, not including the still enormous seed-wastage.

[1] The suggestion that the Lycopod-alliance is wholly distinct from that of the Filicineae (even to the extent of their having a dual origin in Bryophyta (!)) was deduced by Tansley (1907, New Phyt., p. 34) from a consideration of their stelar organization. From the details of the vestigial flagellate retained as antherozoid in these phyla it would appear more probable that their independence is to be traced along a quite different path into the plankton-phase.

The remarkable predominance in all more successful phyla of transmigrants of the utilization of an endogenous meristem as a *cambium* to produce new tissue as xylem and phloem encourages investigation as to the possibility of any analogue being traced in marine vegetation; and the presence of a very similar meristem giving massive axes with seasonal ring-effects in many genera of the Laminariaceae shows that some of the essential factors are already in operation. But there is no need to press the analogy too far; as, for example, to decide whether such centrifugal ringed tissue is to be regarded as the actual homologue of xylem. Land-plants quite clearly have not been evolved from Laminarians, but the latter may present a clue to the evolution of the mechanism. It must not be forgotten that higher land-plants present such merismatic mechanism in two distinct categories, as that of the normal cambium, and again as a phenomenon of quite distinct nature in the very similar meristem known as cork-producing phellogen. These two sets of phenomena can be in no sense regarded as related one to the other, but both may be equally a later successful adaptation of some older mechanism.

The factors in common are (1) the mitotic activity of an initial cell, with (2) the formation of units in radial rows: what happens to these units subsequently has no bearing on the original mechanism.

Analysis of the factors concerned shows that these are the necessary expression of continued growth in any axis in which longitudinal extension no longer obtains; that is to say, they are referable to phenomena of two-dimensional growth. The same mechanism of 'radial rows', following cessation of intercalary growth in length is the commonplace of all massive marine algae (Phaeophyceae and Florideae), though usually presented by the peripheral units. From the latter the case of 'cambium' only differs in being endogenous, and hence giving segments on both sides; this being again an indication that the surface-layers have lost their activities. All these factors are present in an old stem of *Laminaria Cloustoni*, and the repetition of such factors elsewhere among transmigrant phyla gives the possibility of both cambium and phellogen, radial rows and annual rings. Secondary adaptation of the units to special functions, in connexion with water-storage and food-conduction, are secondary physiological details which have no bearing on the essential primary mechanism of organization.

That the vascular system of a Higher Land-Plant may ultimately attain a 'morphology of its own', to be conveniently distinguished as a 'stelar system', is the natural consequence of extensive adaptation to special functions; but it does not imply that the *stele* has any primary existence. A direct analogy may be traced in

(4) Yet in all essentials of transpiration-current, stomatal mechanism, tracheides, protoxylem, cambium, centrifugal and centripetal wood, the general mechanism of xerophytic anatomy runs with striking uniformity, as the expression, it must be concluded, that in all these respects there was only one set of solutions possible for the various new subaerial problems.

Special interest attaches to the case of *Isoëtes* as a test of these generalizations, owing to the special features of the antherozoid in this type, usually described as multiciliate. Figures given by Belajeff (1885), and usually copied, indicate that the flagellation of the rather elongated and spirally twisted zoïd has no relation to the ciliated crest of the Fern-type, but is definitely *octokont*; eight equal and similar flagella, three body-lengths, being inserted together at the anterior end. Such a construction may be a derivative of the isokont construction, as is the case of the *tetrakont* zoïd; but it is wholly distinct from the type of the Fern (cf. Belajeff, Bot. Zeit. 1885, p. 798). It begins to appear that detailed investigation and consideration of the significance of the flagellated phases of the Vascular Cryptogams may yet afford cause for the revision of many long-accepted generalizations; and a broader view may be welcomed as tending to throw light on many stelar problems, as well as on the mode of construction of spore-bearing members.

Finally, as compared with the Bryophyta, the Pteridophyta present a remarkably complementary condition. Assuming the fundamental homology of the original haploid (sexual) and diploid (asexual) generations, the Bryophyta present the somatic deterioration of the sporophyte generation to a mere capsule; the Pteridophyta that of the sexual soma to a vestigial rudiment. The reason for the former is traced in the failure of the absorptive mechanism to become independent, or to give a food-salt supply, as tending to effect starvation-reduction even more than the general decadence to be expected in a parasitic phase. The success of the Fern-sporophyte is solely referable to the evolution of an absorptive *root*; and the deterioration of the prothallus is the expression of its own efficiency in sexual reproduction, which renders it increasingly functional in a 'juvenile-stage', at a level in shoot-construction below that of the organization of *crampon*-axes.

Among Gymnosperms the retention of the aquatic phase is sufficiently exemplified in the flagellated antherozoid of Cycads and *Gingko*; the close agreement of the details of the male prothallus in Conifers suggesting identity of origin, as also in the definite vestigial archegonium-mechanism (*Pinus* and *Ephedra*); though the Gnetales may belong to a distinct series.

But in Angiosperms no direct evidence of the older epochs remains; even the sexual organs of the algal stage are wanting. No homologue of antheridium or archegonium is left, and only the general mechanism of siphonogamy suggests that a similar range of progression must be postulated in the older history of the race. Even more completely than in the highest animals has the Angiosperm eliminated all vestigial relics of the flagellated plankton-phase and its marine existence.

There is no reason to believe that any other mode of algal progression through the subaerial transmigration was possible to autotrophic organism; and it is freely accepted that Angiosperms at some time must have had a cellular female prothallus and archegonia, as well as flagellated antherozoids, even if no trace remains; but it does not follow that they have come down either the Fern or the Lycopod path of progression. The remarkable example of *Lycopodium* and its associates suggests that their algal and benthic ancestors may have been again of a wholly distinct category, and their biological convergence in general

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the study of the animal skeleton, which has attained a very definite morphology of its own, quite regardless of the fact that it is wholly subsidiary to the musculature it is adapted to support; and bones are carefully studied after cleaning away the muscles. Similarly there may be a danger in glorifying the stele, as an abstract identity, at the expense of the tissue it was originated to supply.

features of transpiration-mechanism, shoot-construction, foliage-leaves, and reproductive sporophylls may be similarly inevitable. Pollen-tubes and oospheres, ovules and micropyle, spore-tetrads and asexual diploid phase, again, cannot be explained on any other lines than those of inevitable reproductive phases of progression; the spore-tetrads with included meiotic phenomena being perhaps the last discernible relics of the specialization of Marine Phytobenthon.

Summary. (Pteridophyta.)

(1) A review of the main groups of transmigrant Fungi, Bryophyta and Pteridophyta, emphasizes the isolation of the modern representatives included in these great sections of the Plant Kingdom, as only remotely related to each other, though convergent in many respects, as they acquire similar equipment of the land in closely similar manner, and solve the same problems of the progression along closely identical lines; since all departures are necessarily based on their common ancestral equipment as Marine Phytobenthon. Each group is sharply delimited, both above and below, and the conventional recognition of higher rank expresses the increasing complexity of the factors of such secondary response.

(2) Thus successful transmigrant Fungi, based on a two-phase life-cycle, introduce the evolution of the air-borne spore, as a further development of the asexual unilocular sporangium, with its reduced number of meiotic mitoses, but show little advance in any other directions (beyond the faculty attained by many lichens and some Basidiomycetes of drying up *in toto*, to revive on the addition of water); but all other higher transmigrant races follow essentially the same principles in point of spore-production and dispersal of air-borne perennating units.

(3) The equally circumscribed group of Bryophyta introduces the mechanism of a transpiration current, in the sporophyte generation only, which must be paralleled as an inevitable sequence in all higher autotrophic races. On the other hand, the Pteridophyta, in virtue of more massive marine attachment crampons, initiate the absorbing root-portion of the system; and this, added to the transpiration mechanism of the parasitic zygote, solves for all time the problem of individual absorption from the food-solution, with consequent intimate attachment in the finer texture of the soil. This, in fact, is the great contribution of the Pteridophyta to the story of the progression. Reproductive mechanism of air-borne tetrad spores, as also the sexual phase of fertilization by a flagellated gamete within an archegonium, but continues the older problems as solved in similar fashion by Bryophyta, and the homosporous Pteridophyte is again sharply circumscribed by its own limitations.

(4) Just as the first stages of the transmigration became possible to plants in which reproductive economy in the moving aqueous medium of the sea had attained the limiting case of oogamic fertilization *in situ*, to give a protected, parasitic embryo, 'germinating' *in situ*: so the full domination of the land only becomes possible to advanced types passing through the parallel progression with the Pteridophyta, to similar phases of reproductive economy, as applied to the *asexual* units, combatting the new and terrible wastage-factor of the wind-borne spore. The differentiation of heterospory thus leads in turn to the evolution of the solitary megaspore, non-discharged, hence germinating *in situ*, requiring to be 'pollinated' by the unaltered microspore of another individual, and so working out the inevitable consequences of macro- and microprothallia, wholly enclosed within the parental soma, in close proximity; with the consequent act of cross-fertilization, followed by the parasitic embryonic sporophyte of the

seed-stage, thus at last successfully produced in absence of any external supply of water.

(5) It is this parallelism in progression of the reproductive organs, on which the strain of racial wastage falls more particularly in two succeeding environments of water and air, that constitutes the most attractive feature of the botanical story of the transmigration; as the complete comprehension of this great environmental change alone affords the clue to the inevitability of the parallelism. The two epochs, so efficiently bridged by the two phases of the life-cycle, each presents its own special mechanism of physiological progression, as dealing with the problem of benthic wastage; and the highest expression, as the limiting case, is alone capable of passing to a higher grade of organism.

(6) It now begins to be clear that the essential difference between the two-phase life-cycle of higher plants, and the one-phase cycle of higher animals, is the expression of the fact that in virtue of an easily acquired food-supply (taken ultimately at the expense of autotrophic organism) the pressure of wastage was rarely sufficient in the benthic animal-life of the sea (including the Fish-type) to induce the limiting condition of oogamic fertilization *in situ*; so that in transmigrant animals, although advanced heterogamy may obtain, the gametes are still freely discharged and dispersed in the external medium; while in cases in which fertilization *in situ* is ultimately achieved, the active life, necessitated in the parent with a view to securing its own food-supply, implies the ready separation and discharge of the embryo at some early phase of its career. The spectacle of an individual reproducing while still attached to the parent organism, and at its expense, would not be regarded as a satisfactory physiological solution of the problem of reproduction.

XII

THE ALGAE OF THE TRANSMIGRATION

It may be difficult to realize that the vegetation of the land was originally evolved in all essential factors of morphology, anatomy, and physiology, as the direct and only possible adaptation to autotrophic existence, in a condition of environment diametrically opposed to that in which it lives at present to puzzle the teleologist of the land. That is to say, evolved in an aqueous medium with abundant supplies of salts and carbonic acid, but with little free oxygen and the feeblest light-supply, it has emerged and successfully readjusted its entire mechanism to the requirements of an atmospheric medium, in which the water-problem now appears almost the first cause of all higher specialization (*Xerophyton*). The oxygen-supply is abundant, that of carbonic acid greatly diminished; while the light-supply may be so superabundant that the intense insolation, in absence of a balanced supply of food-salts, particularly of nitrogen compounds, finds expression in the fact that polysaccharide debris accumulates to an enormous extent, and the timber-tree becomes the characteristic type of vegetation for forest-lands with least nitrogen-content.[1]

The story might appear incredible to a subaerial botanist were it not

[1] Russell (1915), 'Soil Conditions and Plant-growth', p. 75.

that identically the same sequence is to be traced with regard to the evolution of the human body, which similarly began as an autotrophic chlorophyll-containing flagellate in the plankton-phase of the surface-water of the primal sea; to become holozoic and dorsiventral as a multicellular benthic organism under the influence of substratum and readily acquired food-material as plankton-rain; to undergo metameric segmentation, the analogue of plant-ramification in the individualized animal-mechanism with a centralized control, and to lift from the substratum as mobile *nekton*, attaining the vertebrate fish-soma adapted for seeking food in cold dimly-lighted water; and at last, passing through the rigours of the subaerial transmigration to rise as an air-breathing organism, ultimately automobile on dry land by a secondary use of marine limbs, to follow the optimum food-supply provided by the advancing land-vegetation; and hence ultimately living at the expense of the fruiting timber-tree of the tropical jungle within the limit of the quasi-historical epoch.[1]

On the other hand, it may be pointed out that the exact agreement of the general histories of these two divergent branches of living organization amplifies the story of the evolution of the earth itself in a manner little grasped by the conventional geologist, who appears to postulate rock and subaerial denudation as the primary factors of his world-scheme. The evidence of the progression of organization as 'life' satisfactorily demonstrates the existence of the primal ocean covering the entire earth-surface, of a constitution as regards salt-content recognizably similar to that of the sea of the present world; and that cytoplasmic life passed through the early phases of the plankton-story many ages before there was any practicable sea-bottom,—that benthic life began with the first rise of such 'benthos' substratum, and not before; following the rise of the sea-bottom to emerge with it as both 'plants' and 'animals' above the sea-surface on the first exposed rock,—that the organisms which passed through the emergence-period to dominate the land were the most highly equipped of the marine forms, as sea-weeds and fishes,—and that both fish and sea-weed, practically as advanced as any in the sea at the present time, are necessarily far older than any sedimentary rock the result of relatively late subaerial denudation. The driving power of this vast machine, which has correlated and controlled these changes in 'inevitable sequence', without any 'breach of continuity', being the progressive cooling of the earth's crust, continued down the ages as the effective 'guiding hand', periodically 'changing the sieve' of Natural Selection, and constituting the causal factor in biological evolution, as in the determination of the physical features of the material substance of the present world-surface.

The preceding chapters may supply a rough sketch of the probable evolution of land-vegetation from marine phytobenthon; the progression of the algal races of the sea, from the condition of the first hypothetical sessile flagellate to build the benthic soma, has been outlined elsewhere; while the still older story of the stages of the evolution of the autotrophic flagellate races of the sea, from 'nothing at all' but the ions of sea-water, may be also dealt with separately. The full recognition of the sequence of these main phases of plant-life is the first requirement of the teaching of modern biological science; and no better introduction to the vegetation of the land can be found than that of the still existing, and largely unaltered, vegetation of the sea. As all botany begins in the sea, so the beginnings of land-phyla pass down to the marine epochs of benthon and plankton, in all probability wholly independently of one another; the most cherished conceptions of

[1] Genesis, i. 29.

affinity may be no more than stages of the inevitable and hence parallel progression, relics of the adaptation of marine organization to problems of subaerial environment faced simultaneously in many advancing higher races. In such a story the evolution of the simple, alternating, 'two-phase' life-cycle of the Bryophyta and Pteridophyta, which has attracted so much attention on the part of land-botanists, appears but a small thing; and emphasis on this part of the story, so familiar in botanical works of the last generation, tends to obscure the greater epic of the rise of the vegetation of the sea, in the sea, to a level at which such transmigration became possible and effective, to give the plant-life of the world, as we ourselves as land-animals first come in contact with it. It is not so much that it is impossible to tell the story of the origin of Land-Flora in any other way than as the rise of a new post-sexual phase, as that the latter suggested solution touches but a minor feature of the progression, and the problem requires to be viewed in a broader perspective.[1]

It remains to briefly review from the story of the survivors what emerges as to the nature of the remarkable algae of the transmigration. One may begin at once by discarding all hopes of ever finding such forms in the fossil state; all knowledge of such vegetation can be only gained by deduction from types still existent in the sea as relics of still older phases of organization, as also from the construction of their more highly modified descendants of the land. Indications of marine equipment are so abundant and complete in both Bryophyta and Pteridophyta, apart from any consideration of the probable independent algal origin of many Phanerogams, that it is not difficult to form some sort of mental picture of the nature of these plants; the most striking feature being that while they were clearly unlike any known Marine Algae of the present world, they were by no means more primitive or elementary. *On the contrary, they appear in fact to have been more highly organized than any* single *algal type at present known to exist in the sea.* This remarkable conclusion is not at variance with general principles; it really throws an interesting light on the present condition of marine algae as being the survivors, few and often only remotely connected, of the races that, for some reason or other, could not pass through the sieve of the transmigration epoch, and so remain practically unchanged in their old environment. The forms which could pass on, passed on, and left no trace in their original station. Thus the conclusion appears well-warranted, even if not unavoidable, that:—

(1) The transmigrant algae of the 'Archegoniate series' were phyla of 'green' Algae, such as might be included within the modern conception of the Chlorophyceae; as expressed not so much in the absence of accessory pigments, which may be readily minimized, as in the special nature of the starch-metabolism in discoid chloroplasts; i.e., neither separating fluid physodes of polysaccharide (Phaeophyceae), nor detaching more solid amylodes (as in the Florideae).

(2) The somatic organization is based on a multiseptate (or parenchymatous) construction, now found only among types of Phaeophyceae, or as a trace only in internodal segmentation of *Chara*, as distinct from the more 'filamentous' organization of the Florideae.

(3) Morphological differentiation had proceeded as far as the specialization of massive main axes, lateral ramification and dichotomy, apical cells or apical meristems, delimitation of bilateral 'leaf'-ramuli, as well as crampon ('root') ramuli, Fibonacci symmetry, and even axillary habit in the laterals, in all respects comparable with what is found only in marine benthic algae (Laminariaceae, Cystoseireae, *Sargassum* Dictyotaceae, and *Chara*).

[1] Bower, 'Origin of Land Flora', 1908, p. 226.

(4) Anatomical progression had given the possibility of secondary increase by a permanent merismatic 'ring', differentiation of internal 'storage' and 'skeletal' tissues, differentiation of living conducting 'perforated' units (phloem); again features characteristic more particularly of the parenchymatous organization of massive Brown Algae, as Laminariaceae.

(5) On the other hand, in Reproductive processes, as representing the mechanism of economizing wastage of the race, fertilization *in situ* had attained a level beyond anything known among Brown Algae, though familiar throughout the Florideae. Similarly the progression of asexuality had been already established as an 'alternation' of haploid and diploid phases, in which the asexual generation had reduced its meiotic sporangium to a limiting tetrad, on a level with the case of the Dictyotaceae among the Brown Algae, as this is also the normal expression of the life-cycle of the tetrasporic Florideae.

In general terms the algae of the transmigration may be roughly visualized as having possessed the metabolic efficiency of the Chlorophyceae, the somatic equipment of the Phaeophyceae, and a reproductive scheme of Life-History more advanced than that of *Dictyota*, though in other respects falling behind that of the modern Florideae, in that these last had eliminated the flagellated zoïd as microgamete in favour of a simple method of 'spermatogamy'. *The algae of the transmigration may be thus said to have combined the best features, as factors of the highest grade of progression, of the known great conventional series of marine phytobenthon, and yet to have belonged to none of them.* On the whole, it is interesting to note that the greatest consensus of such factors may be traced perhaps at present in the still living but clearly vestigial group of the Dictyotaceae, a race of essentially reef-pool forms of Tropical Seas, as again suggestive of the optimum vegetative conditions of warm, relatively quiet and shallow, well-illuminated water, under which such an advance might have been conceivably initiated. In our unavoidable ignorance of the multitude of lost races, there can be no real objection to such a conclusion; but it may be noted that, short of a world-catastrophe, the highest race is never lost; it owes its very existence to the fact that it represents the most successful domination of the external environment. The highest race may pass on to something new and apparently different, but it does not vanish. The point arises, however, where did such a race arise, and what were the special conditions, now wanting, which called forth such a type of marine vegetation, which has not been apparently repeated a second time, or in more modern epochs? The only suggestion that can be adduced is based on the hypothetical mechanism of the rise of sea-bottom to constitute the benthic substratum, and ultimately the first emergent land. The total area of the modern land-surface of the world is only about $\frac{3}{11}$, leaving $\frac{8}{11}$ water. Of the former the scanty coastal fringes supporting a perceptible amount of marine algae is further restricted by sandy and muddy deposits of subaerial denudation, to an extent which is largely responsible for the neglect of sea-weeds as an important factor in botanical progression. The first land which emerged from the sea was presumably rock (including calcareous precipitates and coral-reef), rising gently over great areas of sea-bottom; that is to say, on a continental scale, to which even the area of the modern Sargasso Sea may afford a small comparison. Taking such a benthic area as only 10% of the present land-surface, it would afford a region for the growth of algae, at that time the crowning plant-race, far beyond the possibilities of the area at present available for the benthic life of the sea. One gains an idea of a Benthic or 'Sea-Weed Epoch' of the world's history, in which marine vegetation may be said to have culminated over continental shallow areas,

within a range of 50–100 fathoms from the surface, of which modern sea-weed vegetation is but a relic, often regarded as negligible by oceanographers,[1] and restricted to a merest fringe of the more steeply emergent land-masses; the more so as shallow seas become filled with sedimentary deposits. There is no need at present to emphasize these deductions, the simple facts of the existing types of Brown, Red, and Green Algae, in their isolated characters, remote relationships, and aberrant distribution, express a kaleidoscopic variation of the relatively few elementary factors of benthic existence, in a manner which at the present time appears at first sight wholly meaningless in the environment of the unchanging sea. That the algae of the transmigration were what we should call fine plants, i. e., 3–6 ft. long, since requiring massive attachment-organs, with a capacity for organization beyond that found expressed in any one type or phylum of modern sea-weeds, admits of no reasonable doubt. The survivors of the transmigrant races inherit as the equipment of the sea all the factors of higher organization now found distributed among representatives of widely differing groups; while the extreme specialization of the forms emerging as land-flora again affords the clue to the cause of the non-migration and extreme isolation of such vestigial genera of the border-line as *Chara* and *Fucus* at the present day.

Finally, of all the remaining algae of the sea, it is to the Brown Sea-weeds, or Phaeophyceae, that one has to look for the demonstration of the phases of progression of marine phytobenthon. Green Algae are curiously vestigial, mainly as aberrant coenocytic Siphoneae; the Florideae express an intensified variation-scheme within a wonderfully restricted range; even the most elaborated forms presenting but little advance on the simplest in the factors of their life-cycle, and the mechanism of their reproductive processes. On the other hand, within the relatively few and isolated types of the Phaeophyceae (130 gen. and 1,000 sp.), is included the entire range of progression of benthic life, from the condition of the first Phaeophycean Zoïd which conceivably assumed the immobile cyst-phase on a practicable substratum, to massive organisms of dimensions fully comparable with our own conventional ideas of what a plant should be, as derived from the contemplation of more familiar types of land-vegetation. It is thus by the more intensive investigation of the available types of Brown Algae that one may hope to trace the solution of the more fundamental problems of the advance of autotrophic plant-life beyond the flagellated races of the plankton-phase; and incidentally it may be pointed out that possibly no other country is so well situated for such more detailed investigation of these unique relics of an older world, as the coast of Great Britain, with its mingling of sub-arctic, temperate, and sub-tropical forms.

Before the epic of the stupendous epoch of a world-transmigration, of which only the merest glimpse has been afforded in the preceding pages, older concepts of the origin of land-flora from the vegetation of fresh-water ponds or swamps appear meagre and threadbare; as the reasons for post-sexual sterilization in an environment of increasing difficulty and complexity, or the evolution *de novo* of a new generation presenting so much of the equipment of marine organisms, also appear the more remote and fantastic. The story, as now put forward *for the first time*, may be elaborated at many hands; but few can call in question the wonder of the broader vistas thus opened up for the survey of the older chapters in the progression of biological life on this world.

[1] Cf. 'Challenger' Exped. (1885), 'Botany', vol. I; 'Valdivia' Exped. (1907), II. 2, p. 552.

The full significance of the theory thus outlined is not immediately apparent. For the first time one can give in elementary terms a fairly coherent account of the progression of plant-life on the earth's surface, and not only so, but an equally definite presentation of the sequence and significance of the associated animal phyla, wholly dependent on the autotrophic plant-kingdom for their supply of food and energy, as divergent originally from the elementary autotrophic flagellates of the plankton-phase. With regard to the first and most fundamental problems of life, modern botany has still little to say. The fact that plants as found growing on the land are organized in terms of 'cells', and present, so far as can be seen, wholly unnecessarily elaborated phases of reproduction and life-history, quite different in many respects from human ideas of a simple reproductive cycle, has been established in terms of Cell-Theory of two centuries' growth, but affords no answer to such obvious questions as to why plants, or animals either for the matter of that, are ever made of cells at all. Why the cells should be of a certain size, to the demonstration of which modern microscopes are graded;—why sexual fertilization was ever invented, the meaning of asexual reproduction, or even why a tree is what it is, in terms of stems, roots, branches, and flowers, as opposed to the dorsiventral organization of our own animal bodies;—these are simple queries open to any who begin the study of botany for the first time, soon to be largely shelved, or even obscured under accumulated detail of complex terminology, and a mass of minutiae which have little bearing on fundamental topics. One is taught to laboriously accumulate such detail in the hope of one day being able to understand it.

That 'Life' was initiated in the sea, actually from the substance of ionized sea-water, and from nothing else, to progress in pelagic water to the phase of the 'cell'-unit, as the 'plankton-soma', attaining a definite range of volume in correlation with its advancing organization of nucleus and chloroplasts, flagellated mechanism, binary fission and sexual fusion, follows from the survey of the relics of organism still left on the world in this original environment as the '*Plankton-Phase*'.

The influence of substratum, in affording mechanical assistance to sessile or anchored (*hormon*) organism, is traced in the '*Benthic Phase*' of both plant and animal, culminating in the Sea-weed and the Fish, residual still in modern seas, in which the cell-organization of the plankton-scheme is necessarily retained, with all its essential factors of progression largely unaffected, to assist in the evolution of the massive soma of the benthic plant, with 'members', 'organs', and 'tissues', progressively delimited in accordance with further physiological needs; until in the sea itself one finds autotrophic organisms with the full equipment of what is conventionally understood as a *plant*, from our familiar association with land-vegetation; and again *animals* with the essential equipment also of our own automobile vertebrate bodies. The whole scheme illustrates the parallel progression of such autotrophic and holozoic organism respectively from the stage of the cell to that of the full type of '*soma*' as a complex cellular machine.

The last great world-change, of which we have only indirect knowledge, is that which introduces the factor of 'Land', by the late upheaval of primary rock above the surface of the sea, an event which may be possibly regarded as dimly indicated by the 'Huronian Epoch' of the Geological record; and marine organism is thus brought into direct association with atmospheric air and subaerial environment, to mark out new lines of progression to still higher and more strenuous forms of land life; though these are again necessarily expressed in terms of preceding organization and mechanism. The cells and somatic organization of all land-plants, as also

all their reproductive cycles and mechanism, are but the continuation of the mechanisms evolved in the sea, to suit the conditions of life in the sea, as the best response possible under such conditions; and though the mechanism may be emended, modified, or superseded in innumerable details, the primary plan of the architecture, and the entire range of general principles of organization, remain essentially marine. The more fundamental the main laws of existence, the farther back is their origin to be sought in early benthic phases, the plankton-epoch of the sea, and lastly in the ultimate segregation of living plasma from ionized sea-water.[1]

Taking 'Life' as synonymous with 'organization to the limit of environmental possibility', all further progression to increasingly complex conditions implies somatic differentiation, and specialization of parts; the three main epochs of plant-life on this world present a remarkable story of the progression of the soma from the primary plankton-phase, in which all functions as they are initiated, as (1) mechanism of form-changes, (2) photosynthetic apparatus, (3) locomotor mechanism of flagella, (4) nuclear mechanism of control, are elaborated, appear with increasing differentiation within the confines of the single 'cell'-individual.

Following the attainment of the possibilities of the Benthic phase, the cell-soma is replaced by a 'multicellular' aggregate, in which the same functions are relegated to distinct tracts of units as 'tissues', with further consequences; as, for example, the distinction of photosynthetic and non-photosynthetic tracts implies (1) the initiation of 'conduction', and (2) the delimitation of skeletal and storage-regions. No organism which had not attained to the highest differentiation of the plankton-soma stood any chance of further progression in the benthic state. The Cyanophyceae, for example, remain as relics of attempts at such progression in phyla with imperfect nuclear differentiation, and are hence freely regressive to the plankton-habit at any point.

Similarly at the subaerial transmigration, only the most highly differentiated algae succeeded in making good on the land. Conducting tissues, little more than initiated in the benthic state, become highly complex and 'vascular', thus saving the situation. Irritability, as a vague and general response of the soma to light-changes, is emphasized; the members respond to gravity, as well as to other variations in the new environment; and ultimately a distinction can be traced between perceptive region and mechanism of response, implying in turn a mechanism of conduction of stimulus over considerable ranges of protoplasts. The elaboration of a growing-point in higher algae becomes emphasized as a region dominating all extensions and morphological elaborations of the land-organism, with almost indefinite possibilities of embryonic activity. Tissues, whether mechanical and skeletal, or with the possibilities of secondary meristem, attain a vast range of developmental progression; *but the origins of all the main successful adaptations of the land are to be traced down to the benthic phase of the sea.*

Even more than to factors of progressive somatic organization, since less obviously referable to immediate environmental changes, these generalizations apply to the mechanism of reproduction, as ultimately expressed in complex phenomena of sexuality and the life-cycle. Taking the term '*Reproduction*' as the expression of the insistent physiological need of compensating the wastage of the race, consequent on the death of the individuals,—as their more complex mechanism is worn out, or becomes overloaded with debris of metabolism beyond possibility of elimination,—

[1] Church (1919), 'Building of an Autotrophic Flagellate', Bot. Mem. No I; (1919), 'Plankton Phase and Plankton Rate', Journ. of Bot., Supp. III.

reproduction, as something more than mere binary fission, which survives as the cell-division of higher organism, is traced in the plankton-phase as the first fusion of failing protoplasts; so that out of two old ones, so to speak, it may be possible to rejuvenate one good one. This leads to a complex process involving fusion of the nuclear tracts; but, so far as the sea is concerned, such sexual fusion does not appear to have got beyond the condition of isogamy of equal protoplasts, with as yet no distinction of 'sex'; only in the more advanced of pelagic plankton forms does the complex cell subdivide to smaller recapitulatory units for this purpose (cf. *Corethron*, Diatom; *Peneroplis*, Foraminifer; *Pyrocystis* in the Peridine alliance). Again, only forms with such a reproductive mechanism made good in the benthic phase. 'Non-sexual' Cyanophyceae and Bacteria remain as vestigial phyla on the border-line of the first protobenthon filaments.

But, given the act of fusion and its possibilities, as in hastening, or even regulating, the variation-capacity of the race, there follows the general specialization of units, tissues, and ultimately of entire individuals, to subserve distinct sub-branches of the function; and the subject diverges by dichotomy along very distinct lines.

The sessile benthic phase, of anchored organism (*hormon*), at once introduces a wholly new factor of '*dispersal*', undreamt-of in the case of suspension-plankton of the ever-moving sea. Differentiation along two distinct paths at once supervenes in all advanced phytobenthon, since sexual fusion of even isogamous gametes involves 50% loss by wastage in the number of reproductive units. By the introduction of a '*neuter*' zoïd, as simply exaggerating the normal tendency to 'apogamy' on the part of imperfectly delimited sexual zoïds, dispersal is provided for at the full rate; and 'sexual' and 'asexual' reproduction is progressively differentiated, whether in the form of reproductive units (*Ectocarpus*), organs (Phaeosporeae, generally), or in the limit expressed by distinct individuals (*Zanardinia*, *Dictyota*). Only the largest dominant Fuci and Laminarians of the colder seas maintain the original wastage, with the sexual cells discharged in the medium, and subserving the functions of both fusion and dispersal.

Similarly differentiation along two other divergent paths, marking the familiar '*sex*'-distinction, still conventionally described as 'male' and 'female', as the micro- and mega-gametes, differentiating in function according to mobility *v.* passivity, minimum mass *v.* food-storage for the zygote, is progressively expressed in terms of special reproductive organs, individuals, and ultimately of 'generations'. As the limiting expression of 'sexual' reproduction in terms of a huge oosphere, fertilized by a flagellated spermatozoid, is attained, so the asexual mechanism is more securely established, and the phenomena of meiosis appear intercalated where they may act as a *regulator* of the succession of generations, rather than as a causal factor.

But given such a specialized mechanism of alternation (*Dictyota*, *Cutleria*), the limiting expression of sexual economy in oogamic fertilization *in situ*, so far as it implies germination of the zygote *in situ*, necessarily establishes the alternation of sexual and asexual phases in the life-cycle for all further time: since on the latter now falls the whole burden of the dispersal-problem; and a two-phase cycle becomes normal for all advanced phytobenthon, without any reference to subsequent transmigration.

The story of the transmigration shows, again, that no phylum which had not previously attained to the level of such an alternation stood any chance of surviving the vicissitudes of the new epoch, to make good as Land-Flora. But further progression in subaerial environment follows similarly divergent lines of differentiation. With the incidence of the

dispersal-function on the asexual spore,—as this in turn is relegated to chance dispersal by air-currents, at enormous expense, as opposed to original movements of water,—so specialization follows, from homospory to heterospory, as an 'imitation' or repetition of 'sex'-distinction, along identical lines in terms of mobility and food-storage, as the *microspore* and the *megaspore*; these again specializing in terms of organs (sporangia), sporophylls, floral shoots (monoecism), and whole individuals (dioecism), as the 'sexes' of historical and colloquial plant-terminology. One begins to see that the *single* reproductive differentiation expressed as 'sex' in the case of animals, for whom the locomotile capacities of the individual eliminates the insistence of the dispersal-problem in the race, can give but a feeble and imperfect comprehension of the possibilities of the *three-fold* differentiation of reproductive processes in plants. Primary differentiation of sexuality and asexuality; isolation of cells, organs, and individuals, distinguished as male and female gametes, organs, and individuals, respectively; later specialization of differentiated asexual spores, sporangia, sporophylls, and floral shoots in land-plants; are but three stages in the same story of continued progression of specialization in the same physiological process across three epochs of autotrophic vegetation, advancing to the limit of environmental possibilities in each; and are to be interpreted by tracing the progression from initial stages in the sea; not, as so commonly in the past, by reading analogies from the reproductive mechanism of higher animals, and least of all highly specialized land-insects, into the simpler story of the early Thalassiophyta.

The plant-problem, known as 'Alternation of Generations', and so long regarded as pre-eminently mysterious, or as an academic attribute of higher plants, thus reduces to a simple function of the need for *dispersal* in the case of 'sessile' anchored Hormon-organism; a function of less obvious significance in the animal kingdom, so long as the reproductive units are discharged in the external medium, and the individual organisms, being locomotile at some stage of their career, are so far capable of dispersing themselves. The separation of this function from mere sexual fusion, in terms of two distinct individuals, as 'generations' in the life-cyle, affords a simple case of what it is customary to conventionalize as 'division of labour', in concentrating on one job at a time, as an example of what is really a very obscure analytical property of living organization, which again finds commendable expression in our own methods of attacking similar biological problems.

Concluding Note. The preceding chapters were commenced (1918) as illustrating the general conclusions to be drawn from a consideration of the living vegetation of the sea, as represented more particularly by the series of the Phaeophyceae or Brown Sea-weeds. To the varied types of this group, which in virtue of their parenchymatous (multiseptate) organization expresses most clearly the origin and rise of the benthic soma in the sea, they may serve equally well as an introduction. Since, in no living race of organism is more clearly expressed the inception of the great law of benthic life under which we ourselves, as transmigrant derivatives of the animal benthon of the sea, continue to exist. A clear distinction being drawn for the first time between the life of the individual benthic organism, and that of the race to which it belongs. The former expressed in metabolic somatic organization, the latter in reproductive processes, based on the older fusion-mechanisms of the pelagic plankton, and continued into higher grades of specialization, adapted to the needs of compensating the wastage of such reproduction and dispersal, in a practically limitless and restless medium. Under the benthic scheme of life, thus consequent on the physical factors of the

sea, the whole metabolic activity of the individual soma is spent in working for the good of the race, in order to compensate the wastage-factor, under penalty of racial extinction, and in complete individual ignorance of this natural law. Such conflict between the working value o the organism, ultimately within the power of the central control as a personal factor, and the need of the race, is again only what becomes to our more refined perceptions the elementary distinction between what is 'evil' and what is 'good'; which is which being determined by the mere fact of racial survival under the given circumstances. It is interesting to find that the earliest dawn of such a fundamental law, determining the evolution of the psychology of higher organism and that of the moral code, should be thus emphasized in the life of the first marine algae, to be henceforward increasingly intensified in the increasing struggle of all benthic plant and animal descendants of the plankton-phase, through the stress of the subaerial transmigration to still higher expressions of biological organization, as affording a definite clue to the progression of individuality in benthic organism and the object of individual existence. We are, for example, still isolated human entities, because the effect of wave-action in the surface-waters of the primal ocean involved the minute subdivision of all incipient plankton-phases. And thus, while the Plankton Epoch, which covers the first evolution of the individual entity as a living cell, discloses what may be termed the Planktic Law of self-preservation, and the progress of benthic organism involves conceptions of the 'good of the race', which are subsequently to be crystallized in conceptions of a racial deity, —so the subconscious recognition of the intensified struggle of the subaerial transmigration becomes reflected in theological applications of the general principles of racial progression to the development of our individual controlling consciousness, as expressed in interpretations of an even more drastic change of phase.

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